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**Research in Motion: Patterns of Large-Scale Migration in Dragonflies and Birds**

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# Research in Motion:

# Patterns of Large-Scale Migration in Dragonflies and Birds

**by**

**John Holley Matthews, B.A.**

**Dissertation**

Presented to the Faculty of the Graduate School of

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# Dedication

To my wife and family, for whom this degree has been a sacrifice and distraction, and especially to the members of my family now deceased who encouraged me onwards but never saw the end. You are missed, and I have thought of you often these five years.

# Acknowledgments

I am most grateful to my committee: each of you has provided essential ideas, calming guidance, and (regularly) correction on this wayward path. I cannot imagine this degree without each of you. I am particularly grateful to Camille, who took a chance on an ill-prepared and strange student. I hope I have justified your confidence.

I also wish to acknowledge my parents and sister, who shared their profound love for natural history, a love that hounded me back into science. Along with my wife, they have always served as a reminder that our work must have purpose and meaning and that service is the work that gives our life meaning.

I am also grateful to the many colleagues and mentors who have supported me during graduate school, particularly Megan Biesele, Brian Hickman, Bill Hoffman, Jim Lester, Bob Brick, Philip Corbet, Michael May, Anthony Cognato, and Dennis Paulson. This work would be quite different without you.

**Research in Motion:**
**Patterns of Large-Scale Migration in Dragonflies and Birds**

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Supervisor: Camille Parmesan

The work I present here can be broadly described as focusing on the spatial, temporal, and ecological basis to patterns of movement by highly vagile organisms. From this perspective, the differences between chapters are matters of scale: community versus population ecology, and movement by thousands of birds through two localities versus a study of a single invertebrate species crossing North America.

Animal movement over large scales has proven difficult to study throughout the history of biology. Proximal challenges have largely reflected practical problems with observing spatial displacement in individual organisms. Population-level evolutionary and ecological analyses — ultimate explanations for movement — depend on solutions to those proximal challenges. Here, I have tried to interweave both proximal and ultimate approaches.

Large-scale movement also presents challenges from a conservation perspective. The conservation implications of the final chapter are immediately applicable to avian

researchers and resource managers. In contrast, understanding why and how *Anax junius* Drury (Odonata: Aeshnidae) is moving across North America does not have such direct conservation implications. The species is not endangered, nor have threats to its range or behavior been suggested. My interest instead grew from the need for a model system to explore aquatic invertebrate conservation as well as the practical difficulties of studying long-distance migrants of all kinds, invertebrate and vertebrate. These chapters thus form a whole through their focus on determining how and why organisms move over large spatial scales and the connection of that behavior to habitat.

Many species move great distances during individual lifetimes. Threats from land-use change, habitat fragmentation, and climate shifts will all have — are already having —impacts on many species. We need accurate, inexpensive, and effective tools to be able to count, compare, detect, define, delineate, and explain patterns of movement. I have endeavored to improve a few of these tools and, if possible, provide a few new examples and explanations grounding that movement.

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# Chapter 1

## Characterization of Nuclear Microsatellite Loci for the Common Green Darner Dragonfly *Anax junius* Drury (Odonata: Aeshnidae)[1][2]


**ABSTRACT**

Fourteen polymorphic microsatellite loci were developed from an enriched genomic library of the widely distributed migratory North American dragonfly species, the Common Green darner (*Anax junius).* For a group of 22 larvae, these loci averaged 16 alleles, with individual loci ranging from 9 to 29 alleles. Observed heterozygosity averaged 0.784 per locus.


*Anax junius* is a North American dragonfly found between Guatemala and Canada (Walker 1958, Needham et al. 2000). Larvae follow a "migrant" or "resident" life-history trajectory (Trottier 1971). Migrant larvae emerge by fall and disperse as adults, possibly hundreds of kilometers. Slow-developing resident larvae emerge in spring/summer and disperse more locally (Russell et al. 1996, Matthews 2004, 2005). Freeland et al. (2001) explored phylogeographic patterns using mitochondrial locus CO1, concluding the two dispersal groups were a single species and no spatial patterns could be resolved. Microsatellites were developed to untangle *A. junius* movement and the relationship between phenotypes.

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[1] Portions of this chapter appeared in 2007 as "Isolation and characterization of nuclear microsatellite loci for the common green darner dreagonfly Anax junius (Odonata: Aeshnidae) to constrain patterns of phenotypic and spatial diversity," *Molecular Ecology Notes* 7(5), 845–849.

[2] Sandra Boles, Camille Parmesan, and Thomas Juenger were significant collaborators on this work.

Four microsatellite-enriched libraries were constructed by Genetic Identification Services (GIS, Chatsworth, CA) using pooled genomic DNA. Methods for DNA library construction, enrichment, and screening were as described previously (Jones et al. 2002). Genomic DNA was partially restricted with a cocktail of seven blunt-end cutting enzymes (Rsa I, Hae III, Bsr B1, Pvu II, Stu I, Sca I, Eco RV). Double-stranded adaptor sequences (sequence: 5'-AAGCTTCCGTCGTTTTACAACGTCGTGG) in the size range of 300 to 750 bp were ligated to the restriction fragment ends, which were then subjected to magnetic bead capture (CPG, Inc., Lincoln Park, New Jersey) using 5'-biotinylated $(CA)_8$, $(GA)_8$, $(AAC)_8$, and $(ATG)_8$ capture molecules in a protocol provided by the manufacturer. Captured molecules were amplified and restricted with HindIII to remove the adaptors and ligated into the HindIII site of pUC19. Recombinant molecules were electroporated into *E. coli* DH5∀.

Recombinant clones were selected at random for sequencing, and inserts from individual clones were sequenced with the M13(-24) forward and/or M13 reverse primers using a BigDye terminator Cycle Sequencing kit (Applied Biosystems, Foster City, CA). Enrichment levels were expressed as the fraction of sequences that contained a microsatellite. Sequences were obtained on an ABI 3100 sequencer (Applied Biosystems). Sequenced fragments were screened for the presence of microsatellite repeats using SEQUENCHER 4.1.4 software (Gene Codes). Of the 96 (GA)n clones sequenced, 21 contained microsatellites with more than five repeats, with only three duplicate sequences, yielding 18 candidate loci. Primers for these 18 loci were developed using the server-based software PRIMER 3 (Rozen and Skaletsky 2000) and screened, resulting in fourteen consistently amplifying polymorphic loci.

In 2005, larval *A. junius* were collected from a pond in Port Aransas, Texas (11 individuals), and a pond in Dogtown, Alabama (11 individuals). DNA was extracted from

abdominal tissue using the ChargeSwitch DNA kit (Invitrogen, Carlsbad, CA) following manufacturer instructions. Microsatellite loci were amplified in a Peltier Engine Tetrad 2 Thermal Cycler in 10-µl multiplexed reactions. Each well contained three primer pairs with fluorescently labeled forward primers of HEX and 6-FAM (Integrated DNA Technologies) and NED (Applied Biosystems). These reactions included 3.0 µl dilute DNA template (10 to 50 ng/µl); a 1.3 µl cocktail of three primer pairs (10 µM/µl suspended in a 10mM Tris HCl solution); 0.2 µl water; and 4.0 µl Qiagen Multiplex PCR kit (Valencia, CA), which itself contained 2.4 mM $MgCl_2$, 0.6 U Hotstar *Taq* DNA polymerase (Invitrogen), 0.2 mM dNTPs (Invitrogen), and a 2x proprietary PCR buffer (Invitrogen);. PCR settings were established at 95°C for 15 minutes, then 30 cycles of denaturation (94°C for 30 seconds), annealing (90 seconds at the primer-appropriate annealing temperature), and extension (72°C for 60 seconds). The PCR product underwent a final extension at 60°C for 30 minutes, with fragment analysis completed on an ABI Genescan 3730 sequencer (Applied Biosystems), sized with a custom standard, and genotyped via GENEMARKER 1.50 software.

Scores were analyzed using GENALEX 6.0 software (Peakall and Smouse 2006) and GENEPOP 3.4 software (Raymond and Rousset 1995) (see Table 1–1). GENALEX suggested that all but two loci were in Hardy-Weinberg equilibrium (HWE) following Bonferroni corrections ($p<0.005$). No linkage disequilibrium was observed using GenePop 3.4 (dememorization: 1000, number of batches: 10, number of iterations per batch: 1000) following Bonferroni correction. Six loci showed higher heterozygosity than expected, with a relatively high allelic diversity (9 to 29 alleles; mean: 16.1), probably reflecting unrelated females laying eggs within each pond. We now hope to use these markers to reveal large-scale migratory patterns across North America and to determine the genetic basis for dispersal phenotype.

## LITERATURE CITED


Freeland, J.R., M. May, R. Lodge, and K.F. Conrad. 2003. Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner (*Anax junius*). *Ecological Entomology* 28(4):413–421.

Jones, K.C., K.L. Levine, and J.D. Banks. 2002. Characterization of 11 polymorphic tetranucleotide microsatellites for forensic applications in California elk (*Cervus elaphus Canadensis). Molecular Ecology Notes* 2, 425–427.

Matthews, J.H. 2004. Report on *Anax junius* emergence in Caledon, Ontario, in 2003. *Ontario Odonata,* vol. 5.

Matthews, J.H. 2005. Long-distance migration and emergence patterns in *Anax junius*: review of work to date. *Argia* 17(3), 29–30.

Needham, J.G., M. J. Westfall, and M.L. May. 2000. *Dragonflies of North America*. Gainesville, FL: Scientific Publishers.

Peakall, R., and P.E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Popuation genetic software for teaching and research. *Molecular Ecology Notes* (6(1), 288–295.

Raymond, M., and F. Rousset. 1995. GENEPOP: population genetics software for exact tests and ecumenism. *Journal of Heredity* 86(3): 248–49.

Russell, R.W., M.L. May, K.L. Soltesz, and J.W. Fitzpatrick. 1998. Massive swarm migrations of dragonflies (Odonata) in Eastern North America. *American Midland Naturalist* 140:325-342.

Rozen, S., and H.J. Skaletsky. 2000. Primer3 on the WWW for general users and for biologist programmers. In S. Krawetz and S. Misener (eds), *Bioinformatics Methods and Protocols: Methods in Molecular Biology*. Humana Press, Totowa, NJ, pp 365-386. Source code available at http://fokker.wi.mit.edu/primer3/.

Trottier, R. 1971. Effect of temperature on the life-cycle of *Anax junius* (Odonata: Aeshnidae) in Canada. *Canadian Entomologist* 103: 1671-1683.

Walker, E.M. 1958. *The Odonata of Canada and Alaska*. Vol. 2. Toronto: University of Toronto Press.

Table 1–1. Primer description, amplification conditions, and allelic variability of 14 loci developed for Common Green darners (*Anax junius)*. Included are locus name, locus sequence, accession number, repeat motif, annealing temperature ($T_a$), number of observed alleles ($N_A$), expected ($H_E$) and observed ($H_O$) heterozygosity, Hardy-Weinberg *p* value following Bonferroni correction, and fragment size range (A).

| Locus | Primer sequence (5'–3') | Repeat motif (5'–3') | $T_a$ (°C) | $N_A$ | $H_e$ | $H_o$ | Hardy-Weinberg P value | A (Size range) |
|---|---|---|---|---|---|---|---|---|
| Aj1 | CATGCAAGCTTCTGATGGAA | $(TG)_{14}T$ | 53.30 | 7 | 0.568 | 0.609 | 0.788 | 97–137 |
| | GTGTCGCAAGGGAGAGAGAG | | | | | | | |
| Aj2 | AAATGGTTGAGAAACGAAGCA | $(GA)_6AT(AG)_4$ | 53.02 | 17 | 0.898 | 0.783 | 0.447 | 136–200 |
| | AGACCTCAACTCCGCTTTCA | | | | | | | |
| Aj3 | GAGGGACTTTGGAATGCTGA | $(GA)_{16}$ | 54.80 | 15 | 0.872 | 0.870 | 0.997 | 165–216 |
| | ATGCGTCCGTGATCCTTTAC | | | | | | | |
| Aj4 | GCAGAAGGAAGGACGAAGTG | $(AG)_4(AAAG)_2(AG)_{23}$ | 55.69 | 18 | 0.916 | 0.718 | 0.000 | 136-169 |
| | CGCTTCTCCCTCTGCATTTA | | | | | | | |
| Aj6 | CGGGAGAGAAAATGAACAGC | $(GA)_{15}$ | 53.76 | 17 | 0.875 | 0.609 | 0.010 | 192–260 |
| | AGACAGGCTTTTCGCTCTTG | | | | | | | |
| Aj7 | AGAGGGGGAAAGAAGTCTCG | $(GA)_2A(GA)_8$ | 56.02 | 9 | 0.680 | 0.926 | 0.012 | 213–71 |
| | TCTCAACGCCGTTTCTCTTT | | | | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Aj8 | GACAGCCCTGGTCTCTCTTG | $(CT)_{15}C$ | 57.34 | 17 | 0.904 | 0.913 | 0.689 | 209–61 |
| | GGGGGAGAGAGATATATATAGAAAGG | | | | | | | |
| Aj10 | GAATAGTTCCCCACCTCTTGC | $(CT)_2CC(CT)_{14}$ | 55.42 | 11 | 0.886 | 0.700 | 0.031 | 261–79 |
| | AAATAATTCCGCTGCTTTCG | | | | | | | |
| Aj11 | CTCTCCCTACCTCCCATTCC | $(CT)_{18}$ | 56.27 | 18 | 0.857 | 0.692 | 0.000 | 202-253 |
| | CACCCGTTCTCCCATAAGAA | | | | | | | |
| Aj13 | GATTAAGCGCGAGAGGTGAC | $(AG)_4(AAAG)_2(AG)_6(AAAG)_2(AG)_6(AAAG)_2(AG)_9$ | 55.72 | 27 | 0.946 | 0.955 | 0.127 | 227–99 |
| | CTGTAGCGGTAATGGCTTCC | | | | | | | |
| Aj14 | ATCGGCTTAATCAGGAAGCA | $(AG)_3GG(AG)_5$ | 54.05 | 12 | 0.863 | 0.700 | 0.347 | 265–347 |
| | TTACGCTTCTCCGCATCTTT | | | | | | | |
| Aj15 | CCTCCCCTAAAGACGACTCC | $(TC)_{12}$ | 56.60 | 19 | 0.909 | 0.696 | 0.005 | 283–347 |
| | GCGGAGAGGACAACAAAGAG | | | | | | | |
| Aj16 | GGACTACGGCGTGAAGAGAG | $(GA)_{15}$ | 57.16 | 29 | 0.913 | 0.950 | 0.011 | 285-344 |
| | GCACACCAACACACAACTCC | | | | | | | |
| Aj18 | GCGATCCCAAAAACGAATAA | $(GT)_7GCG(TG)_5$ | 51.23 | 9 | 0.808 | 0.850 | 0.620 | 366-381 |
| | GAGTAATTGGCCTCGTGCAT | | | | | | | |

# Chapter 2

## Continental-Scale Migration by a North American Dragonfly Revealed by Population Genetic and Stable and Radiogenic Isotopes[1]


### ABSTRACT

Large-scale insect movement has proven extremely difficult to characterize. *Anax junius,* a common North American dragonfly species, has long been suspected of engaging in movement over thousands of kilometers. Here, we test the hypothesis that *A. junius* engages in seasonal large-scale movement across eastern North America using a combination of microsatellite loci and stable and radiogenic isotopic ratios applied to a single set of adults. We show that the species forms a single population over more than 30° of latitude, with effective southern movement by individual adults in the fall averaging 909 km and ranging up to 2800 km. A much smaller group of adults showed evidence of a spring northward movement. Individual flying in clusters consist of mixed groups of unrelated individuals from different and noncoastal natal regions. This study constitutes the first evidence for long-distance seasonal migration in the order Odonata. We also provide a novel synergistic model for exploring insect movement applicable to continental scales.


### INTRODUCTION

Long-distance movement by insects is exceedingly difficult to trace directly (Wassenaar & Hobson 2001, Webster et al. 2002), which has limited the study of the patterns and

[1] Thomas Juenger, Leonard I. Wassenaar, Larry Mack, and Jay Banner were significant collaborators on this work.

adaptive basis of large-scale insect movement. Only a handful of purported long-distance insect migrants have been studied. Although dragonflies (order Odonata) have been the subject of limited studies into their movement patterns, many odonate species combine the strongly nektonic and gliding flight rare among other insect taxa (Dingle 1996, Dudley 2002). For over half a century, some 17 North American dragonfly species have been suspected of seasonal movement by individuals over scales of hundreds to thousands of kilometers (Williams 1957, Russell et al. 1998).

The basis for large-scale movement in insects has a long history of scientific debate. Terms such as *migration* and *dispersal* are widely used without clarification or consistency, though each invokes distinct evolutionary ecological explanations. Dispersal is insect movement away from a conspecific aggregation, implying a reduction in conspecific density and metapopulation colonization processes (Clobert 2001); dispersal need not refer to a special mode or set of behaviors associated with the movement. In contrast, migration in an ecological sense is undistracted and persistent movement (Johnson 1960, Southwood 1962, Kennedy 1985), bounded by distinct behavioral/physiological states before and during migrant movement (Dingle 1996). Migration typically occurs between habitat types or ephemeral resources, such as between breeding and overwintering sites.

*Anax junius* (family Aeshnidae) is a widespread North American dragonfly that has been a particular object of speculation given fall movements on the order of millions of individuals passing single locales over a matter of hours (reviewed in Russell et al. 1998). Studies of mitochondrial haplotypes at a single locus revealed no significant population structure across North America (Freeland et al. 2003). A small telemetry study tracked movement by 14 adults, showing typical daily fall movement on a scale of 10s of kilometers. One individual wearing a transmitter weighing one-third its body mass managed to fly 137 km in a single day though other individuals remained at or near the

collection site during the 10-day lifetime of each transmitter battery (Wikelski et al. 2006). Such studies are limited in scope, with small sample sizes, limited numbers of collection sites, intrusive transmitters, and limited battery life, all of which are largely technical and financial problems. Telemetry studies may also conflate total movement (the actual path taken by an organism) with net movement (the shortest distance between the start and end of movement). Brownian motion, for instance, could register as long total movement but little or no net movement. Such issues led Holland et al. (2006) to conclude that more extensive telemetry studies were required in order to speculate about the scope, adaptive basis, and evolutionary ecology of *A. junius* movement.

A promising solution to this problem is through the reading of intrinsic organismal traits. Multilocus genotyping, for instance, can measure phylogeographic patterns and history and define populations, connectivity patterns, and demographic (Avise 2000). The study of movement with genetic markers is essentially transgenerational (Webster et al. 2002), showing the distribution patterns of alleles across a landscape. More recently, the development of extrinsic character analyses based on stable and radiogenic isotopes has revealed detailed intra-generational movement such as migration origin sites (Wassenaar & Hobson 1998) and corridors (Dockx et al. 2004).

The use of $^{2}H/^{1}H$ ratios has been especially powerful for dispersal studies since these ratios vary in precipitation are translated into body tissue through diet in a predictable north-south gradient throughout most of North America, and so can resolve migrant origination sites within a few degrees of latitude (Wassenaar & Hobson 1998, Hobson 1999, Kelly et al. 2002, Lott et al. 2003, Meehan et al. 2004, Bowen et al. 2005). Like almost all odonates, *A. junius* larvae are fully aquatic in a single pond or wetland until emergence and are opportunistic carnivores (Corbet 1962, 1999). Therefore, their tissues will reflect an averaging of multiple $^{2}H/^{1}H$ dietary sources and ambient $\delta D$ values (Hobson et al. 2004).

A more recent trend has been to employ trace element radiogenic isotope proxies, such as those of strontium isotope ratios ($^{87}Sr/^{86}Sr$) (Capo et al. 1998). Terrestrial soil distribution patterns of strontium isotopes can detectably vary over small spatial scales (10s to 100s m), but marine strontium $^{87}Sr/^{86}Sr$ ratios are highly uniform worldwide (Capo & Depaolo 1992, Faure & Mensing 2005). In aquatic systems, strontium ratios enable discrimination between freshwater, estuarine, and marine systems in anadromous and catadromous fish. These systems are distinguishable because marine $^{87}Sr$ and $^{86}Sr$ are typically found in a distinct ratio (Capo et al. 1998, Kennedy et al. 2000). Indeed, mean marine Sr concentrations (7.74 ppm) are more than 100 times mean worldwide river ratios (0.07 ppm) (Faure & Mensing 2005). Such high levels of marine Sr swamp freshwater wetland $^{87}Sr/^{86}Sr$ ratios in near-coastal systems and facilitate discrimination between adults that developed from coastal wetlands from those that developed in wetlands far from coastal zones. Unlike stable isotopes, fractionation through physiological processes and across trophic levels is negligible (Banner and Kaufman 1994, Blum et al. 2000). In other words, strontium ratios in coastal and near-coastal dragonfly wings should reflect a marine or near-marine value and can distinguish an adult that has emerged from a coastal region from one that developed in a more inland area.

Only a handful of movement studies have synergistically combined both intrinsic and extrinsic markers for a single set of individuals (Chamberlain et al. 1997, Clegg et al. 2003, Dockx et al. 2004). Almost all of these studies have focused on distinguishing between distinct breeding and/or overwintering regions in a handful of Neotropical bird migrants, most of whom are members of the family Parulidae.

## METHODS AND ANALYSES

### Sampling Regime

Accurate estimates of population structure should be spatially comprehensive and collected over a relatively short interval (Waples & Gaggiotti 2006), particularly if the species in question might be capable of rapid large-scale dispersal (Wikelski et al. 2006 ). Published reports of mass *A. junius* movement show that concentration zones consistently occur in areas such as narrow projections of land (e.g., barrier islands or isthmuses) bounded by large bodies of water (e.g., estuaries, bays, very large lakes) and/or sudden elevational shifts (e.g., mountain passes, coastal ranges) (Lamborn 1890, Russell et al. 1998). Particular localities with regularly large fall mass movements include several south-pointing peninsulas, such as Point Pelee, Ontario, Canada, and Cape May, New Jersey, USA (Russell et al. 1998). Similar concentration zones are also typical Neotropical bird migrant traps (Rappole 1995). Inland areas appear to have less consistent densities of adult *A. junius* than coastal areas. Anecdotal evidence and personal observations suggest that mass sightings in inland areas may be best characterized as foraging or mating groups rather than the focused and undistracted movement more typical of migration behavior generally (Dingle 1996); migration in inland areas may more diffuse, occurring at low densities. Sampling at 10 sites was conducted between 30 August and 17 October 2005 between Holiday Beach, Ontario, Canada (45° N latitude), along the Atlantic and Gulf coasts, and south to Chachalaca, Veracruz, Mexico (19° N latitude; Figure 2–1). The selected route focused on wetlands near probable or known concentration zones. Adults were collected with an aerial net, sexed, graded for wing condition, and stored in glassine envelopes. In total, 183 adults were captured, 24% of which were female. The relatively lower rate of capture for females is typical for adults; females tend to avoid the kinds of wetlands used as collection sites unless they wish to mate or oviposit (Buskirk and Sherman 1985).


Figure 2–1. Collection sites in eastern North America.

## MICROSATELLITE DNA DEVELOPMENT AND APPLICATION

Nuclear microsatellite DNA, which consists of short tandem repetitive nucleotide sequences, are ideal markers for studying recent demographic and evolutionary processes given that these loci are diploid, codominant, and often neutral. Primers were developed for nine loci to enable population genetic analysis (Matthews et al. in press). Genepop 3.2 was used to test Hardy-Weinberg Equilibrium (HWE) assumptions for these loci (Raymond and Rousset 1995). All 183 individuals used for genetic analysis were stored in 100% ethanol prior to extraction. DNA extraction, PCR, and analysis methods for these loci are detailed in Matthews et al. (in press). Allelic diversity and observed vs. expected heterozygosity were calculated via GenAlEx 6.0 (Peakall & Smouse 2006).

*Fst* is one of Wright's F-statistics that measures the variability of subpopulations relative to the total population based on genetic variability (Wright 1951, Cockerham & Weir 1987). Overall Fst and significance of pairwise Fst estimates were calculated using GenAlEx 6.0, using 1000 bootstrapped iterations. Pairwise Fst was also calculated for non-geographic groupings. For instance, the collection sites were treated as "populations," and the two sexes were treated likewise in a separate analysis. Pairwise matrices of geographic and genetic distance were also compared via a Mantel test to

explore isolation-by-distance relationships (discussed by Weir 1996, Rouset 1997, and calculated using GenAlEx 6.0 via 100 iterations).

Microsatellite genotypes were also analyzed at the level of individuals rather than pre-defined populations. This procedure allowed testing for the optimal grouping of individuals into distinct reproductive units using Bayesian clustering methods (Pritchard et al. 2000, Gaggiotti et al. 2004). A central issue with such analytical approaches is selection of the most likely number of population clusters and individual assignment within clusters (Waples & Gaggiotti 2006, Latch et al. 2006). Clustering was performed using Structure 2.2 (Pritchard et al. 2000), and optimal clustering was determined by both variance of assignment likelihood (Evanno et al. 2005) and the mode of the posterior probability.

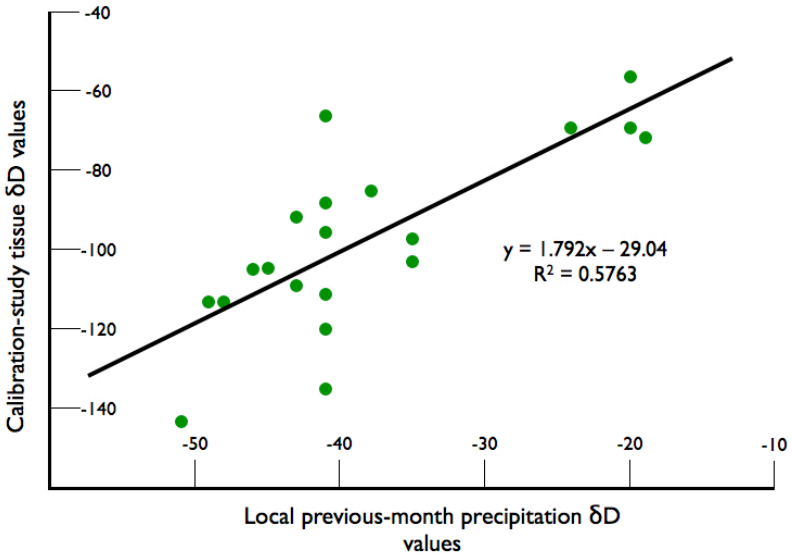


Figure 2–2. The regression of larval and adult tissues collected from calibration-site ponds against mean previous-month precipitation δD values.

**Stable Isotope Techniques**

Adult *A. junius* wings are relatively inert and unmodified following emergence. Adults captured in the field (N = 183) were kept alive in glassine envelopes for up to 24 hours to purge their digestive tract, then one wing was removed and soaked in a 2:1 solution of

chloroform:methanol until reaching the laboratory. Wings (keratin) were cleaned of surface oils using a 2:1 chloroform:methanol solution and then dried in a fume hood. Stable isotope assays were performed at Environment Canada in Saskatoon (National Hydrology Research Center). Stable-hydrogen isotope analyses of samples (δD) were measured using the comparative equilibration method described by Wassenaar and Hobson (2000). Briefly, δD measurements were made on $H_2$ derived from high-temperature flash pyrolysis of wings using a GV Instruments Isoprime. Repeated analyses of calibrated in-house keratin reference materials yielded an external precision of better than ±2‰. Twenty-eight samples were replicated, with a mean difference between replications of 0‰ and two standard deviations (2σ) of ±11‰. Measurements are reported in the δ-notation relative to the VSMOW standard.

For calibration purposes, water samples as well as larvae, adults, and final exuviae were collected from ponds in Austin, Texas, USA, and Caledon, Ontario, Canada over the full emergence season (up to 11 months in Texas and 3 months in Ontario). Tissue samples were found to match most closely the local previous-month's mean precipitation δD as calculated by waterisotopes.org (Bowen et al. 2005; Figure 2–2). Given the wetlands these larvae favor, ambient δD values may evolve too rapidly as a result of evaporation and precipitation events to play a strong influence on tissue δD, while the prey items consumed by carnivorous larvae may, like the prey of insectivorous birds, effectively represent an average of mean local precipitation hydrogen inputs that eventually become incorporated within larval tissue (Wassenaar & Hobson 2000).

Adults are not observed to remain near their natal pond during fall, and fall emergence begins in late July or August at 45° N latitude (Trottier 1971) and extends through September at 30° N latitude (personal observation). A regression of August precipitation δD values across the full extent of the study area (between 71 and 94° W longitude and 18° and 57.5° N latitude) shows a predominantly latitudinal gradient

(p<0.001) (Figure 2–3). These precipitation trends serve as a baseline for the determination of natal pond δD values to infer latitudinal movement.

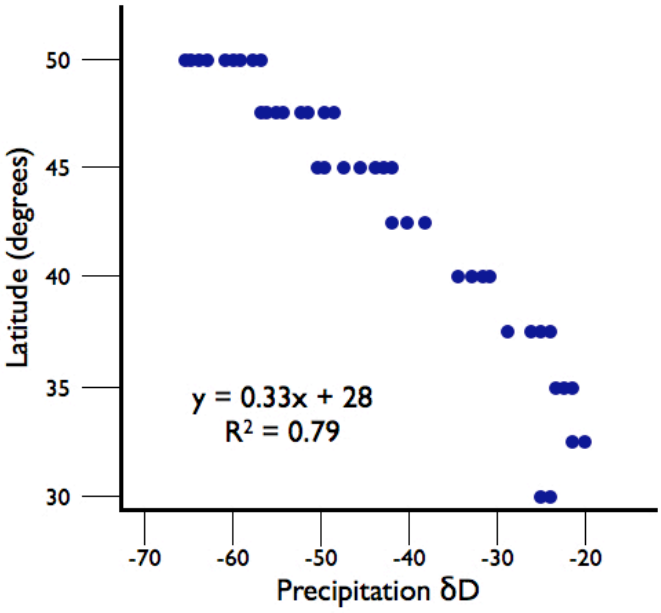


Figure 2–3. The regression of mean August precipitation δD values against latitude.

**Sr Isotope Techniques**

As with the δD techniques, we assumed that adult *A. junius* wing $^{87}Sr/^{86}Sr$ ratios should match the ambient water values of the natal pond and remain inert and unfractionated into the adult stage (Banner & Kaufman 1994, Blum et al. 2000). Wing samples from 19 adult *A. junius* collected over a five-day period at Cape May, NJ, were stored and cleaned as described for δD analysis. Wing tissue was dissolved in concentrated $HNO_3$ and $H_2O_2$ while heated in a conventional consumer-grade 750W turntable microwave oven (following protocols from Nicholson et al. 1989). Strontium was then separated from the sample matrix using Eichrom Sr-spec resin and mounted on rhenium filaments for analysis.

Strontium isotope analyses were conducted at the University of Texas at Austin with a Finnigan-MAT 261 thermal ionization mass spectrometer in static multi-collection mode. $^{87}Sr/^{86}Sr$ ratios are corrected for fractionation to $^{87}Sr/^{86}Sr = 0.1194$ using an exponential law. This correction procedure corrects for mass-dependent fractionation that occurs during analysis and in nature. Replicate analyses of tissue samples were not possible given low tissue concentrations of strontium. Three analyses of NBS SRM 987

conducted while running samples yielded a mean $^{87}Sr/^{86}Sr$ ratio of 0.710239. Raw mass spectrometry data was corrected for rubidium interference and to determine instrumental precision for two standard deviations (2σ); mean sample correction was ±0.00001.

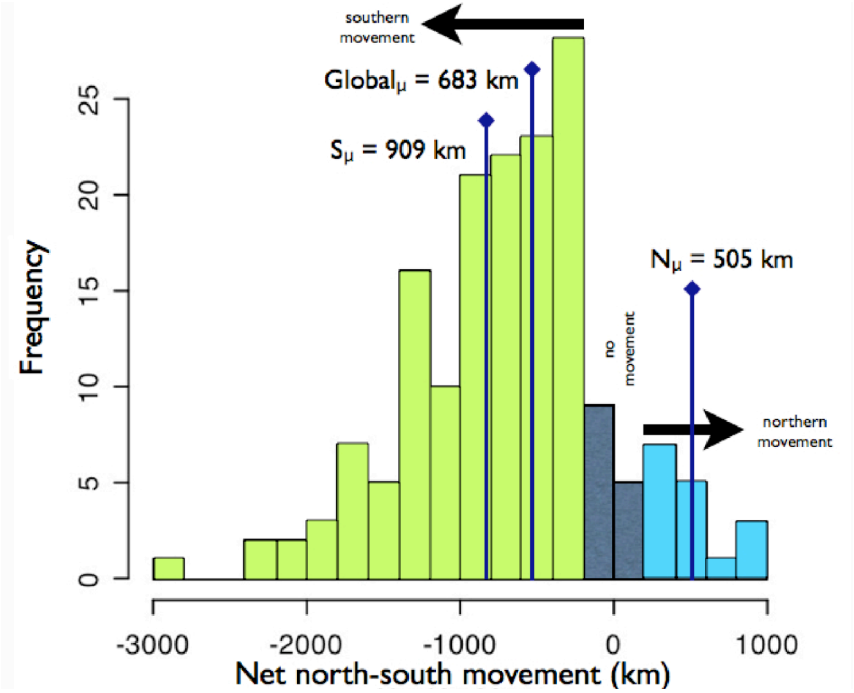


Figure 2–4. A histogram comparing relative degrees of net north-south movement, based upon δD values.

## RESULTS

### δD Structure

A histogram of the normalized number of kilometers moved north-south forms a roughly normal distribution around a mean of -683 km (i.e., a mean southward movement prior to collection of 683 km), with a range of -2800 to +900 km (Figure 2–4). Latitudinal confidence intervals (2σ) were also generated for all individuals (Figure 2–5). Adult natal ponds could be located across a broad swatch of eastern North America, generally following a north-south cline (Figure 2–6). Mean southbound movement out of the range of analytical error was 909 km (n: 134), and mean northbound movement was 558 km (n: 11). One collection site was distinct from the others: all eight individuals collected at the beginning of the fall transect in Holiday Beach, Ontario, had moved north to that

region(mean northbound distance before collection: 540 km) (Figure 2–7). Thus, while this group lacked genetic distinctiveness, it represents possible northern movement.

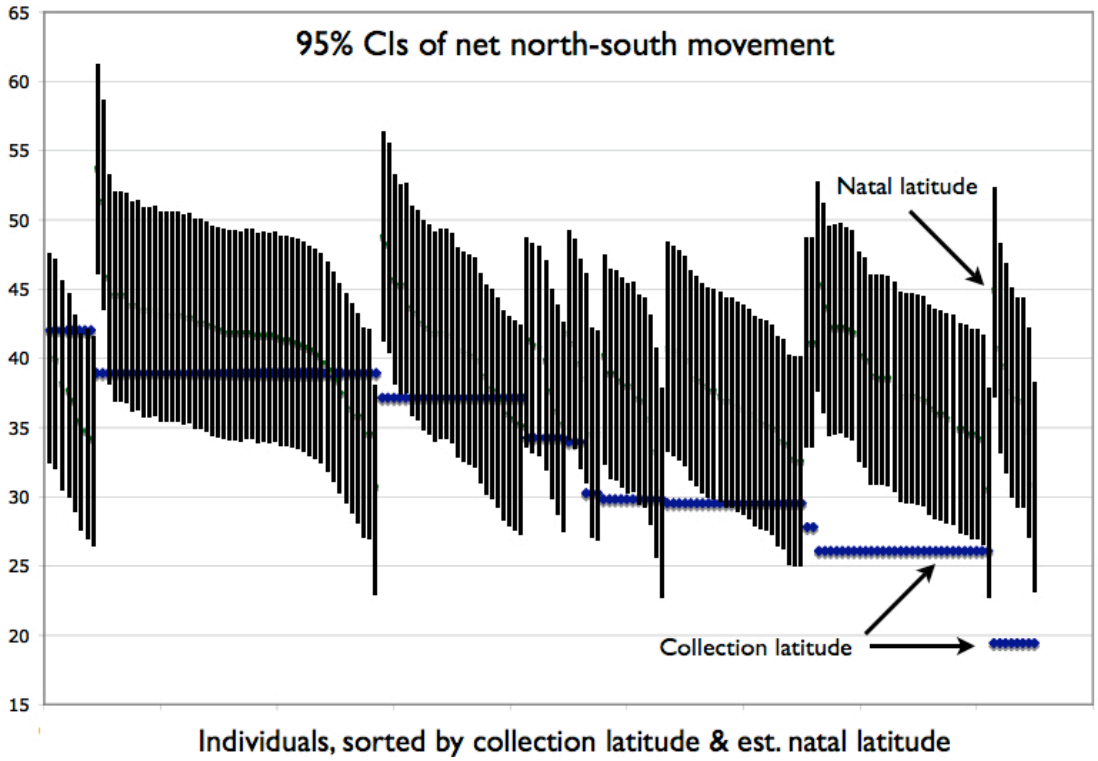


Figure 2–5. Confidence intervals for natal ponds of adult migrant *A. junius,* as inferred from wing δD values, ±95% from the green points. The vertical axis shows latitude, while the blue diamonds reflect the latitude of collection.

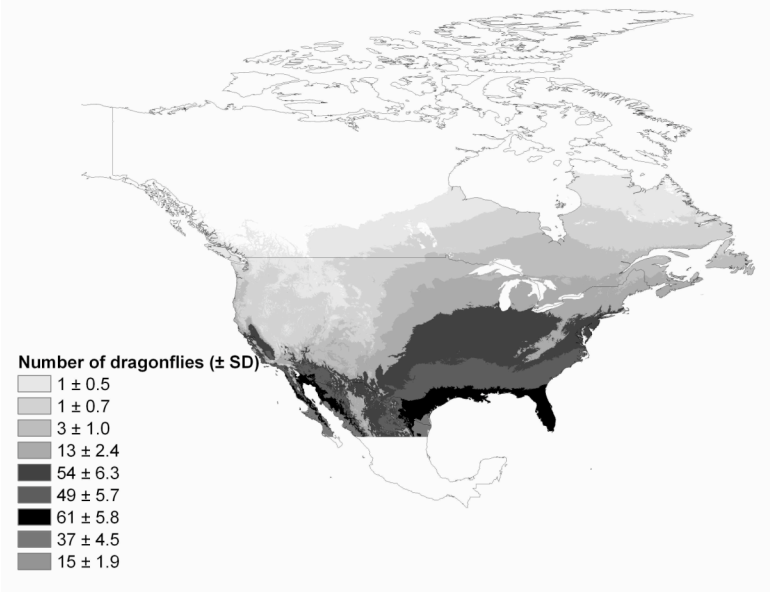


Figure 2–6. Geographic histogram for natal ponds of migrating adults, based on wing δD values.

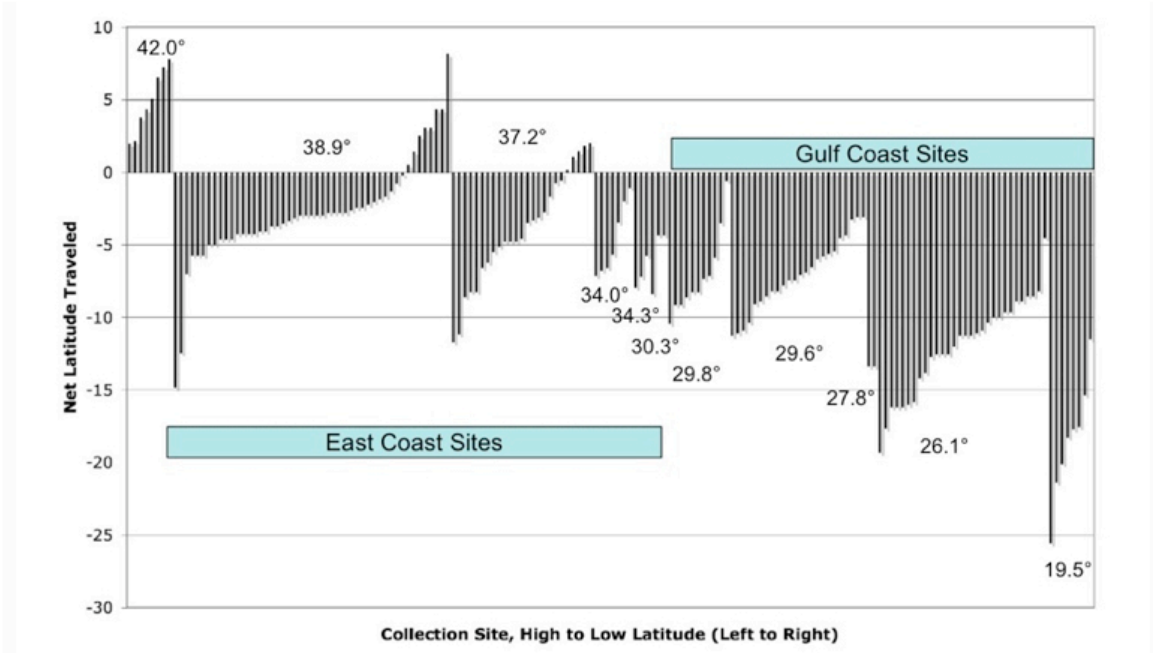


Figure 2–7. Net north-south latitudinal movement relative to collection site, arranged on an X axis from high latitude (left) to low latitude (right), showing southern movement (above the X axis) to northern movement (below the X axis) within each site.

**Genetic Parameters and Population Structure**

All microsatellite loci were highly polymorphic from the sampled locations, with the average number of alleles per locus ranging from 4 to 18 (mean: 10). No significant linkage disequilibrium was found between the nine loci used for analytical purposes ($p>0.05$). Observed heterozygosity ($H_o$) was lower than expected for all loci, ranging between 56 and 94% of $H_e$ (mean: 82%). All loci deviated from HWE ($p<0.001$).

Global Fst among collection sites was estimated at 0.038. When used as the basis for an analyses of molecular variance (AMOVA), each method of categorization explained 4 and 2% of variation respectively (n = 173 individuals, 999 permutations, $p<0.001$).

A Mantel test showed no effect of isolation-by-distance (Figure 2–8). Null alleles are often a concern with microsatellite loci, with many observers speculating that heterozygosity may be systemically undercounted with microsatellites. However, global Fst was also estimated by taking account of null alleles using a new analytical model by Chapuis and Estoup (in press). This adjusted estimate differed by less than 4% from the unadjusted estimate of Fst=0.02 (95% confidence intervals, 0.01 and 0.03).

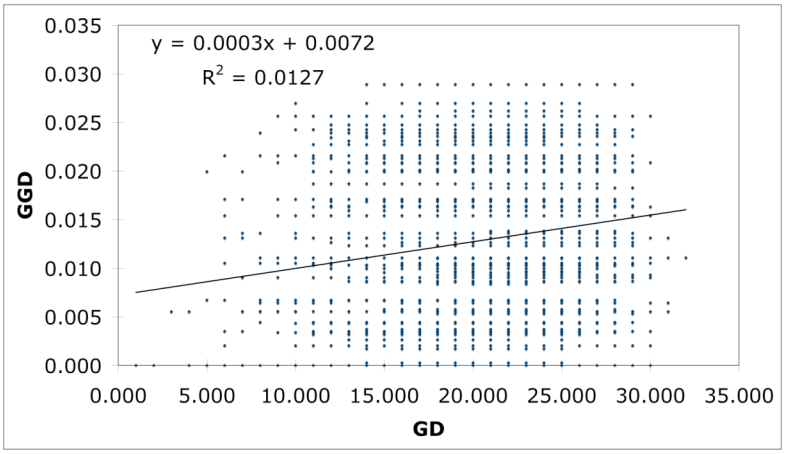


Figure 2–8. A Mantel test comparing geographic distance (GGD) and genetic distance (GD) of migrant adults.

Analysis of $\Delta K$ variance of Bayesian clustering (Evanno et al. 2005) chose the optimal number of populations as two, while the posterior probability of the likelihood

selected an optimum of 11 populations. Any given individual for a particular solution of *K*, however, can possess partial membership in more than one Structure-defined populations. Most individuals have such admixture, with only 30% of individuals having more than 60% membership in any single Structure-defined population. Notably, these "majority membership" individuals fell into only four populations. The remaining 70% of individuals were admixtures of the other seven populations, suggesting that these methods of selection the optimal clustering differed primarily in their population assignment resolution rather than in presenting fundamentally different solutions. No relationship was found between sex or MI for the two-population solution, and sex was also an nonsignificant factor for the 11-population solution. However, for the 11-population solution, population assignments for northbound migrants differed significantly from south-bound migrants ($p<0.05$). Pairwise Fst between Structure-defined populations ranged between 0.02 and 0.08.

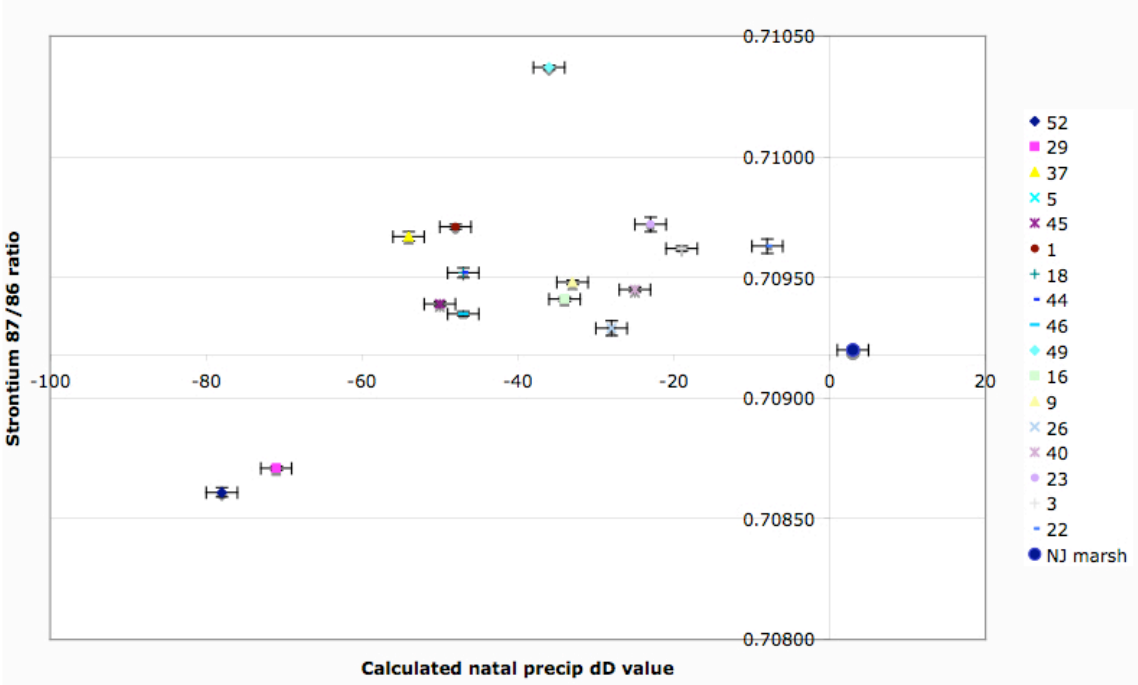


Figure 2–9. $^{87}Sr/^{86}Sr$ ratios plotted against δD values for individual adult wings. The intersection of the X axis on the Y axis is the worldwide marine $^{87}Sr/^{86}Sr$ ratio. δD values range from low and near coastal values (on the right) with more depleted values (on the left), suggesting greater migratory distances.

### $^{87}Sr/^{86}Sr$ and δD Structure

All adults that underwent $^{87}Sr/^{86}Sr$ analysis were also analyzed for δD values (Figure 2–9). None of the 19 had wing ratios that were within the analytical uncertainty of the marine $^{87}Sr/^{86}Sr$ ratio. Indeed, all δD values reflected southbound movement to the collection site at Cape May, NJ, with all but two $^{87}Sr/^{86}Sr$ ratios well above the marine ratio, with δD values reflecting movement from the north of Cape May, NJ.

## DISCUSSION

### Large Net Distances Traveled and High Rates of Gene Flow

The most important conclusions to draw from the synthesis of these methodologies are (1) that individual *A. junius* adults are migrating regularly hundreds (and up to several thousand) of kilometers, and (2) that this movement consists of a southerly fall movement. Presumably this means that a "round trip" is achieved over two or more generations. The histogram of normalized net north-south movement suggests that adults pursue at least two movement strategies: north-bound (positive) and south-bound (negative) movement, with a small but distinct group of individuals (n: 24) that had a MI within the analytical error of not significantly different from 0, or no movement. Notably, the distances estimated here represent *net* movement. Previous work on *A. junius* migration using telemetry to track individual flights showed movement by one individual up to 500 km over a two-week period (Wikelski et al. 2006), but this distance represents the actual path traveled, much like on automobile's odometer. An object undergoing random Brownian motion, for instance, will "travel" thousands of times its body length without moving any effective "net" distance. From this perspective, the net north-south movement of the farthest-traveling individual studied by Wikelski et al. (2006) translated

to only 110 km. In the most extreme case, one adult male captured at 19°N latitude (near Veracruz, Mexico) originated movement at a natal pond between 37.3° and 52.6° N latitude, resulting in a straight-line flight of between 1988 and 3684 km (mean: 2836 km). The *actual* paths traveled by individuals in our study could be several times larger than the net north-south movement we derived.

Further, *A. junius* movement matches the classic definitions of migration as articulated through Johnson (1960), Kennedy (1985), and Dingle (1996) of persistent, undistracted motion. There are very few documented long-distance insect migrants, and none for whom we can make realistic comparisons based on the fine-scaled population genetic data used here. However, we can infer that this movement is quite unlike that of most Neotropical bird migrants; rather than delaying the onset of reproduction, individuals are reproducing throughout the migratory process and they are mating with multiple individuals, who are themselves from potentially very distant natal ponds.

Holland and colleagues (2006) speculated that there might be "universal rules" of migration for orientation or the start and cessation of movement for species as diverse as Neotropical birds and *A. junius*. Within the framework of formally defined migration, adults are leaving their migrant state, probably on a daily basis (personal observation), for the migratory "distractions" of feeding, roosting, habitat guarding by males, mating, and ovipositioning by females. Physiologically, such a combination of behaviors must be intensely draining, and the result must be high adult mortality during periods of migratory movement. Our results indicate that most individuals are moving over scales of hundreds of kilometers and a few are traveling thousands, effectively resulting in a latitudinal leapfrogging (Webster et al. 2002). Even so, some individuals are moving remarkable distances to the south in fall.

**A Single Eastern North America Population**

Based solely on adult microsatellite data, our results clearly show that there is only a single North American "population" of *A. junius* east of about 100° longitude. The high degree of gene flow implied by low continental-scale interpopulation differences of 4% that we found in our study of *A. junius* adults is unusual relative to other taxa, but such rates are not unheard of in species showing high rates of individual movement over large spatial scales. The European eel (*Anguilla anguilla)*, for instance, exhibits interpopulation differences of 0.2% and quite similar Ho/He ratios and deviations from Hardy-Weinberg Equilibrium as seen here (Wirth & Bernatchez 2001). Although coarse measures of gene flow such as mitochondrial and allozyme loci have found little or no population structure in highly vagile species, these markers have much lower resolution than the microsatellites used in our study. As shown with *A. anguilla,* high-resolution markers can eliminate the appearance of panmixia. The patterns exhibited by *A. junius* in this study have not previously been observed in an insect using either fine-scale molecular markers or over such a large scale (>26° latitude). The population structure thus derived is shallow and highly reticulate, suggesting that landscape-level movement is common in *A. junius*, that males and females mate and oviposit multiple times and to multiple individuals. The strontium data from Cape May, NJ, shows that single swarms are composed of individuals from a wide range of sites, so that each assortment of adults in a given site is relatively random.

Moreover, the finding that northern movement occurs in the spring prevents the genotypic "drain" from individual populations seen in other insect dispersers (Hanski et al. 2004), that would remove genotypes from northern mating pools over time. In effect, North American east of 100° longitude *A. junius* adults are migrants, differing only in their developmental phenology and migration direction.

There are several remaining questions that would also be best addressed with multilocus genotyping. Given the temporal and spatial constraints of this study, no samples were taken from far western portions of North America or from islands with known local populations of *A. junius*, such as Hawaii and the Caribbean. Some anecdotal evidence suggests trans-Gulf of Mexico movement by *A. junius* (Russell 2005), so Caribbean populations may prove part of the greater eastern North American population as well. For migrant species found across North America, large-scale migration patterns often show distinct patterns east and west of the Rocky Mountains, with many western migrants engaging in altitudinal rather than latitudinal movement. The semi-arid Great Plains and Great Basin also provides are far more restrictive range of suitable habitat for *A. junius* larvae than the more mesic western portions of the North America. Thus, western individuals are expected to show a stronger degree of population structure relative to eastern individuals.

Moreover, in many species individuals migrating over large latitudinal or altitudinal ranges alter their movement behavior upon reaching the tropics or subtropics from boreal and temperate zones, or individuals with different dispersal phenotypes become more common, such as residency strategies (Rappole 1995). Thus, individuals sampled from the Yucatan peninsula or Guatemala may show more isolation than what was seen over the rest of the sampled range. Although field observations of *A. junius* clearly document multiple matings by both females and males (Buskirk and Sherman 1985) with females producing in excess of 1500 eggs (personal observation), some female odonates store sperm (Corbet 1999), reducing the net impact of multiple matings. Confirmation of multiple paternities among the offspring of single females would be novel and interesting.

**Northern vs. Southern Movement in Fall Adults**

Some 82% of adults sampled showed evidence of southbound movement, but about 6% moved north. Almost all of these individuals were collected at the first and northern-most migrant concentration zone in southern Ontario. *Anax junius* show two distinct emergence patterns, with a spring emergence period separated by some weeks from a fall emergence period (Trottier 1971, Paulson and Jenner 1971, Wissinger 1988, Russell et al. 1998). These emergence groups show quite separate developmental trajectories (discussed in Corbet 1999). While we were unable to determine the time of emergence of the adults collected in Ontario, these individuals seem likely to be older and to have emerged in the spring group at some locality to the south and then migrated northwards. Clearly, this is an area for additional work. Moreover, an observer collecting *A. junius* seasonal movement data at this site for the past 15 years reported that mass southbound swarming did not begin until six days after collection was completed at this site (Paul Pratt, personal communication).

The conclusion that spring-emergent adults are northbound migrants goes against much of the presumption in literature on aeshnids in general and *A. junius* in particular dating back at least half a century (Walker 1958). While late-summer– and fall-emerging adults have been traditionally been called "migrants," spring emerging adults are usually referred to as "nonmigrants" or "residents" (Trottier 1971, Russell et al. 1998, Corbet 1999, Matthews 2005), under the presumption that the spring cohort did not engage in large-scale movement and either remained near the natal pond or perhaps engaged in a much more limited and less directed (but potentially northerly) form of movement (Soltesz et al. 1995). If there was a northern-movement, it must be diffuse, lacking in the notable swarms associated with fall.

An intriguing aspect of the isotopic data is that the males and females show no difference in mean south- and north-bound movement. This pattern is counterintuitive

and also goes against much of the literature on the basis of insect dispersal patterns and the presumption that males and females will pursue different post-emergence movement strategies (Rankin et al. 1986, Bilton et al. 2001). If such differences exist in *A. junius,* they cannot be resolved through fine-scaled multilocus genotyping and in long-distance movement patterns as measured by δD. This also suggests that both males and females are hedging their reproductive bets. Given that *A. junius* are normally associated with small fish-free standing-water systems, multiple ovipositions may help avoid or minimize predation or to reduce the threat of local and regional droughts, which would particularly threaten the habitats favored by the species.

**Migrating Swarms Consist of Unrelated Individuals from Largely Noncoastal Localities**

To determine if swarms of *A. junius* adults consisted of individuals traveling together from some common pond, latitude, or region, we plotted wing $^{87}Sr/^{86}Sr$ ratios against δD values for 19 individuals collected at Cape May, NJ (Figure 2–9). The δD value provided an estimate for how much relative north-south movement an adult had traveled, while the $^{87}Sr/^{86}Sr$ ratio could detect adults that had developed in wetlands in near-coastal regions, where *A. junius* larvae are particularly abundant. δD values suggested that all of these 19 individuals had moved south from their natal ponds, and that none of them had $^{87}Sr/^{86}Sr$ ratios within the analytical range of a marine Sr ratio (represented by the X axis in Figure 2–9). All but two individuals had $^{87}Sr/^{86}Sr$ ratios well above a marine ratio. Two individuals, however, had ratios well below the X axis, implying that they originated their migration in aquatic systems located on or near carbonates derived from ancient seawater. Moreover, these individuals had the most-depleted δD values, suggesting that they had flown the greatest distance to Cape May, NJ, of the individuals collected in this sample (approximating 12.4 to 14.8° net north-south latitude or 1382 to 1685 km).

The application of $^{87}Sr/^{86}Sr$ isotopes to terrestrial movement studies is particularly novel and unusual. In effect, we are using $^{87}Sr/^{86}Sr$ ratios to determine where *A. junius* adults have *not* come from rather than, as in the case of δD values, some imputed origination site. There are a handful of studies that show regional trends in freshwater $^{87}Sr/^{86}Sr$ values (e.g., Wadleigh et al. 1985), but these studies tend to be coarse and problematic when applied to animal movement studies, particularly since $^{87}Sr/^{86}Sr$ ratios can vary over very small spatial scales (Banner 2004).

**Methodological Implications for the Study of Movement**

While the movement of small-bodied organisms has been tracked and studied frequently before, no previous study has been able to make such a rapid advance in understanding the patterns of that movement over such a large spatial scale. The novelty in this study was the application of multiple methodologies producing discrete but complementary kinds of information. Moreover, the use of proxy rather than direct measures of movement enabled much higher samples sizes than previous studies of insects. Direct measures of movement by individual organisms may produce information about fine-scale temporal and spatial patterns but to date they have also largely lacked the power and ability to observe without also modifying the processes of that movement as a result of the monitoring efforts. The use of telemetry for large-scale insect movement research, for instance, may need to wait a bit longer for the development of technology that does not demonstrably interfere with flight metabolism and wing loading and transmits signals that can reliably be detected by observers over large scales. Moreover, real-time methods are particularly good at resolving actual paths, while proxy methods such as were used in this study could be characterized as showing net or effective movement.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**

Avise, J.C. 2000. *Phylogeography: the history and formation of species*. Cambridge, MA: Harvard University Press.

Banner, J.L. 2004. Radiogenic isotopes: systematics and applications to earth surface processes and chemical stratigraphy. *Earth-Science Reviews* 65, 141–194.

Banner, J.L., and J. Kaufman. 1994. The isotopic record of ocean chemistry and diagenesis as preserved in non-luminescent brachiopods from Missippian carbonate rocks, Illinois and Missouri. *Bulletin of the Geological Society of America* 106, 1074–1082.

Bilton, D.T., J. R. Freeland, and Okamura. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32, 159–181.

Blum, J., E.H. Taliaferro, M.T Weisse, and R.T.Holmes. 2000. Changes in Sr/Ca, Ba/Ca and $^{87}Sr/^{86}Sr$ ratios between trophic levels in two forest ecosystems in the northeastern U.S.A. *Biogeochemistry* 49, 87-101.

Bowen G. J., L. I. Wassenaar, and K.A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* **143**, 337-348.

Buskirk, R.E., and K.J. Sherman. 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Florida Entomology* 68(1), 39–51.

Capo, R. C. and DePaolo, D. J., 1992, Homogeneity of Sr isotopes in the oceans. *EOS, Trans. Amer. Geophys. Union*, v. 73, p. 272.

Capo, R.C., B.W. Stewart, and O.A. Chadwick. 1998. Strontium isotopes as tracers of ecosystem processes: theory and methods. *Geoderma* 82(1), 197–225.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry, and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.

Chapuis, M.P., and A. Estoup. In press. Microsatellite null alleles and estimation of population differentiation. *Molecular Biology and Evolution*

Clegg, S.M., J.F. Kelly, M. Kimura, and T.B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology* 12, 819–830.

Clobert, J. 2001. Introduction. In *Dispersal,* edited by J. Clobert. New York: Oxford University Press.

Cockerham, C.C., and B.S. Weir. 1987. Correlations, descent measures: drift with migration and mutation. *Proceedings of the National Academy of Sciences* 84(23), 8512–8514.

Corbet, P.S. 1962. *A biology of dragonflies*. London, UK: HF & G. Witherby.

Corbet, P.S. 1999. *Dragonflies: behavior and ecology of Odonata*. Ithaca: Cornell University Press.

Dingle, H. 1996. *Migration: the biology of life on the move*. New York: Oxford University Press.

Dockx, C., L.P. Brower, L.I. Wassenaar, and K.A. Hobson. 2004. Do North American Monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. *Ecological Applications* 14(4), 1106–1114.

Dudley, R. 2002. *The biomechanics of insect flight*. Princeton, NJ: Princeton University Press.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software Structure: a simulation study. *Molecular Ecology* 14(8), 2611–2620.

Faure, G., and T.M. Mensing. 2005. *Isotopes: principles and applications*. Third edition. Hoboken, NJ: John Wiley & Sons.

Freeland, J., M. May, R. Lodge, and K.F. Conrad. 2003. Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner *Anax junius*. *Ecological Entomology* 28, 413–421.

Gaggiotti, O., S.P. Brooks, W. Amos, and J. Harwood. 2004. Combining demographic, environmental and genetic data to test hypotheses about colonization events in metapopulations. *Molecular Ecology* 13(4), 811–825.

Hanski, I., C. Erlahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7(10), 958–966.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326.

Hobson, K.A., G.J. Bowen, L.I. Wassenaar, Y. Ferrand, and H. Lormee. 2004. Using stable hydrogen and isotope measurements of feathers to infer geographical origins of European birds. *Oecologia* 141, 477–488.

Holland, R.A., M. Wikelski, and D.S. Wilcove. 2006. How and why do insects migrate? *Science* 313(5788), 794–796.

Johnson, C. G. 1960. Migration and dispersal of insects by flight. *Nature* 186, 348–350.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M. Finch. 2002. Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130, 216–221.

Kennedy, B.P., J.D. Blum, C.L. Folt, and K.H. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences*

Kennedy, J.S. 1985. Migration, behavioral and ecological. Pp. 5–26 in M.A. Rankin (ed.), *Migrations: Mechanisms and adaptive significance*. Institute of Marine Science, University of Texas, Austin.

Lamborn, R.H. (ed). 1890. *Dragonflies vs. mosquitoes*. New York: D. Appleton & Co.

Latch, E.K., G. Dharmarajan, J.C. Glaubitz, O.E. Rhodes. 2006. Relative performance of Bayesian clustering software for inferring substructure and individual assignment at low levels of population differentiation. *Conservation Genetics* 7, 295–302.

Lott, C.A., T.D. Meehan, and J.A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. *Oecologia* 134(4), 505–510.

Matthews, J. 2005. Long-distance migration and emergence patterns in *Anax junius*: review of work to date. *Argia* 17(3), 29–30.

Matthews, J.H., S. Boles, C. Parmesan, and T. Juenger. In press. Isolation and characterization of nuclear microsatellite loci for the common green darner dragonfly *Anax junius* (Odonata: Aeshnidae) to constrain patterns of phenotypic and spatial diversity. *Molecular Ecology Notes*

Meehan, T.D., J.T. Giermakowski, and P.M. Cryan. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental and Health Studies* 40(4), 291–300.

Nicholson, J.R.P., M.G. Savory, J. Savory, M.R. Willis. 1989. Micro-quantity tissue digestion for metal measurements by use of a microwave for an acid-digestion bomb. *Clinical Chemistry* 35(3), 488–490.

Paulson, D.R., and C.E. Jenner. 1971. Population structure in overwintering larval odonata in North Carolina in relation to adult flight season. *Ecology* 52(1): 96–107.

Peakall, R., and P.E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Popuation genetic software for teaching and research. *Molecular Ecology Notes* (6(1), 288–295.

Pritchard, J.K., M. Stephens and P. J. Donnelly, 2000. Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959.

Rankin, M. A., McAnelly, M. L., Bodenhamer, J. E. 1986. The oogenesis-flight syndrome revisted. In Insect flight: Dispersal and migration , ed. W. Danthanarrayana. pp. 27-48. Heidelberg and Berlin: Springer-Verlag.

Rappole, J.H. 1995. *The ecology of migrant birds: a Neotropical perspective*. Washington, DC: Smithsonian Institution Press.

Raymond, M., and F. Rousset. 1995. GENEPOP: population genetics software for exact tests and ecumenism. *Journal of Heredity* 86(3): 248–49.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145:1219-1228.

Russell, R.W. 2005. *Interactions between migrating birds and offshore oil and gas platforms in the northern Gulf of Mexico: Final Report*. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2005-009.

Soltesz, K., B. Barber, and G. Carpenter. 1995. A spring dragonfly migration in the Northeast. *Argia* 7(3):10-14.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 37, 171–214.

Trottier, R. 1970. Effect of temperature and humidity of the emergence of *Anax junius* in Canada. PhD dissertation. University of Toronto, Toronto, Ontario, Canada.

Trottier, R. 1971. Effect of temperature on the life-cycle of *Anax junius* in Canada. *Journal of Canadian Entomology* 103, 1671–83.

Wadleigh, M.A., J. Veizer, and C. Brooks. 1985. Strontium and its isotopes in Canadian rivers: fluxes and global implications. *Geochimica et Cosmochimica Act* 49, 1727–36.Weir, B.S. 1996. *Genetic data analysis II*. Sunderland, MA: Sinauer Associates.

Walker, E.M. 1958. *The Odonata of Canada and Alaska*. Vol. 2. Toronto: University of Toronto Press.

Waples, R.S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for evaluating the number of gene pools and their degree of connectivity. *Molecular Ecology* 15(6), 1419–1439.

Wassenaar, L.I., and K.A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *NAS Proc* 95(26): 15436-39.

Wassenaar, L.I., and K.A. Hobson. 2000. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39(3), 211–217.

Wassenaar, L.I., and K.A. Hobson. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology* 35(9), 1845–1850.

Webster, M.S., P.P. Marra, S.M. Haig, S. Bensch, and R.T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17(2): 76–83

Weir, B.S. 1996. *Genetic data analysis II*. Sunderland, MA: Sinauer Associates.

Wikelski, M., D. Moskowitz, J.S. Adelman, J. Cochrain, D.S. Wilcove, and M.L. May. 2006. Simple rules guide dragonfly migration. *Biology Letters* 2(3), 325–329.

Williams, C.B. 1957. Insect migration. *Annual Review of Entomology* 2, 163–180.

Wirth, T., and L. Bernatchez. 2001. Genetic evidence against panmixia in the European eel. *Nature* 409(6823), 1037–1040.

Wissinger, S.A. 1988. Life history and size structure of larval dragonfly populations. *Journal of the North American Benthic Society* 7, 13-28.

Wright, S. The genetical structure of populations. *Annals of Eugenics* 15, 323–354.

# Chapter 3

## Large-scale Dragonfly Migration by *Anax junius* (Odonata: Aeshnidae) Results in Genetic Homogeneity Across Temporally and Spatially Discrete Populations[1]


### ABSTRACT

Reproductive isolation by time and distance are normally presumed to foster genetic differentiation. Though widely distributed across North America, we found that *Anax junius* larvae and adults exhibit little population structure. The species also shows two distinct but sympatric life-history patterns, producing two types of adults with potential temporal reproductive isolation. We show that larvae and adults also demonstrate little genetic differentiation between these life-history groups. These findings are likely explained by the ability of adult *A. junius* to disperse across environmentally heterogeneous regions and to mate with multiple partners during the movement process, blurring genetic boundaries and creating a shallow continental-scale population structure. Our results suggest that multiple life-history patterns that promote temporal and spatial reproductive isolation can be maintained over large spatial scales by movement patterns.


### INTRODUCTION

Historically, highly structured populations have been assumed to follow from reproductive isolation, whether that isolation was induced by temporal (e.g., Pascarella 2007) or spatial segregation, as from a geographic barrier (e.g., Lessios and Cunningham

[1] Thomas Juenger was a significant collaborator on this work.

1990). In contrast, low levels of population structuring are associated with vagile species (Wirth and Bernatchez 2001, Funk et al. in press), population mixing events independent of dispersal strategy (Florin & Höglund 2007), and iteroparous multi-partner mating strategies (Kenchington et al. 2006), even when measured with high-resolution markers such as nuclear microsatellite DNA. Most of patterns of population structuring follow patterns derived from distinct life-history strategies (Cole 1954). Weak or shallow population structure patterns, however, have clear trade-offs in the potential for populations to adapt to local conditions, particularly when a species' range limits span large geographic scales with correspondingly high levels of habitat heterogeneity.

Self-directed nektonic long-distance dispersal appears to be a rare behavior among insects (Williams 1957, Dudley 2000), but a handful of dragonfly species (Order: Odonata, suborder: Anisoptera) have long been suspected of large-scale seasonal migration (Russell et al. 1998). Of this group, the North American dragonfly *Anax junius* is arguably the best studied, with recent studies suggesting that single individuals are capable of dispersing >100 km/day (Russell 2005, Wikelski et al. 2006), and a nested clade analysis of mitochondrial sequences found no significant geographic structuring across North America (Freeland et al. 2003). At least one study has suggested that both male and female adult *A. junius* are iteroparous (Buskirk and Sherman 1985).

Moreover, *A. junius* engages in a bivoltine (two generations annually) emergence pattern over most of its range (15 to 50° N latitude; Needham et al. 2000). All larval development takes place within a single wetland (see Figure 3–1). One generation, traditionally referred to as "residents," begins development in summer or fall, enters a quiescent stage during winter, reinitiates larval growth during the spring, and emerges as a teneral adult in late spring or early summer (Trottier 1971, Russell et al. 1998). These adults are believed to pursue a relatively local adult movement strategy, remaining near their natal pond, though some anecdotal reports exist for spring migration by spring-

emergent adults (Soltesz et al. 1995). A second generation, usually termed "migrants," begins development in late spring and reaches maturity by the end of summer or beginning of fall. In contrast to residents, migrants are believed to engage in a fall southerly migration (Russell et al. 1998). Both migrants and residents may be found within a single wetland. These patterns were first documented by Trottier (1970, 1971), though many subsequent studies have documented these life-history patterns and phenologies across eastern North America (e.g., Paulson 1966, Wissinger 1988, Russell et al. 1998, Matthews 2004; reviewed in Corbet 1999). While at the extremes of the range, only one life-history pattern may dominate (Trottier 1966, Catling 2004), the sympatric bivoltine pattern has been documented between 19° (Matthews, unpublished data) and 45° N latitude (Catling 2004). Beginning with Trottier (1970, 1971), migrants and residents have been described as separate populations, even when referring to individuals found within the same pond, which implies some significant degree of reproductive isolation.

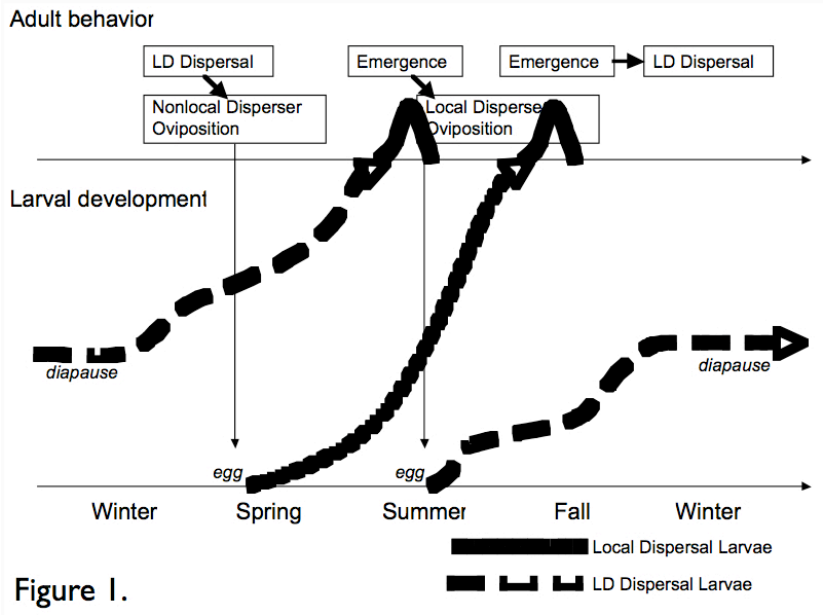


Figure 3–1. *Anax junius* life cycle development, following Trottier (1971) and Corbet (1999).

Taken together, these life-history patterns lead to quite different predictions for North American *A. junius* phylogeography as well as genetic differentiation between so-called resident and migrant adults. Reproduction is believed to occur multiple times for both males and females, and specific females have been observed over small spatial scales (<1 $km^2$) laying eggs at multiple sites within a single pond and at multiple ponds in a single locality (Buskirk & Sherman 1985). However, while these behaviors might lead to a reticulate population structure over small spatial scales in individuals with limited dispersal behaviors, egglaying patterns over larger scales are not known. In many long-distance migrant species, particularly migrant insect species, migration is a distinct form of movement behavior that precedes mating and/or egglaying and often occurs during a distinct life stage. Thus, migration leads to outcrossing and metapopulation structures (e.g., Rankin et al. 1986, Hastings & Harrison 1994, Bilton et al. 2001, Hanski et al. 2003, Freeland et al. 2005). Over smaller spatial scales, migration may be more likely to alternate with mating/egglaying behaviors in an iterative fashion (e.g., Dingle 1996). If the reproductive patterns seen in *A. junius* adults at small spatial scales are also followed at large scales, then long-distance migration might lead to a shallow or weak population structure that mirrors, at best, migration corridors following major physiographic barriers or major nesting or overwintering grounds, if they exist. Thus, large-scale movement by reproductive adults should result in a shallow population structure.

In contrast, the two life-history patterns should promote genetic differentiation. Although adult lifespan has not been determined definitively for *A. junius,* for most odonates the adult stage lasts between a few weeks and a few months. The distinct emergence periods of spring-emergent residents and fall-emergent migrants should form a temporal reproductive barrier that at least severely restricts mating between spring-emergent residents and fall-emergent migrants to a brief mid-summer period.

Support for either result is limited. Indeed, little phylogeographic work has been done with odonates at any scale. Small- to medium-scale population genetics work suggests that poor-dispersing species develop metapopulation structures (e.g., Rouquette & Thompson 2007). Large-scale dragonfly phylogeography has previously been restricted to the use of the single mitochondrial locus cytochrome oxidase 1 (CO1). *Libellula quadrimaculata* (family: Libellulidae) is a cosmopolitan Holarctic species that is occasionally observed in mass aggregations and is suspected of being a long-distance fall migrant (Russell et al. 1998). A study of continental-scale haplotype variation found only 1–2% haplotype variation over very large spatial scales (Artiss 2004).

*Anax junius* (family: Aeshnidae) is arguably a much better flyer than *L. quadrimaculata* (Walker 1958, Russell et al. 1998). Freeland and colleagues (2003) sampled individuals collected over a range of years and seasons and lumped adults and larvae together in their analysis; they found no significant spatial component to population structure. They also found no distinction between migrants and residents. While the geographic scope was very broad — samples ranged between Newfoundland, Canada, and Hawaii, USA —movement by individuals over large scales could confound gene flow given the effective sampling period. Moreover, the collection site of adults and larvae differ profoundly in their implications for population genetics. Larval movement is restricted to a single, often small (<1 hectare), body of standing water (Trottier 1971, Matthews 2005), whereas the collection site of an adult may not be very informative of its natal pond. Thus, combining adults and larvae may present confounding views of population structure in a species in which large-scale movement is restricted to a single life stage. A study of larval population structure should be more capable of resolving admixed individuals, while larvae and adults in a single analysis group may not distinguish between variation within and between collection sites.

Further, mitochondrial studies may not have the same power of resolution as other kinds of molecular markers for highly vagile organisms (Crochet 2000). Allozyme and mitochondrial evidence suggested was panmictic the European eel (*Anguilla anguilla)*, while multilocus nuclear markers successfully measured very weak but statistically significant population structure (global Fst < 0.001) matching natal river populations (Wirth and Bernatchez 2001).

The most effective way of distinguishing between hypotheses about *A. junius* large-scale movement, population structure, and developmental paths is through the use of fine-scaled, neutral, and codominant markers. Odonates have only recently received attention from molecular ecologists, but nuclear microsatellite primers were recently developed for *A. junius* (Matthews et al. in press). These markers enable an exploration of the interplay between dispersal and life-history from a new perspective at high resolution.

Using nuclear microsatellite DNA primers, we test the hypotheses that larval *A. junius* will be the best means of exploring continental phylogeography given high rates of large-scale adult movement, and that adult movement should overrule temporal segregation of migrant and resident life-history patterns and intergenerational adult-larvae differences, resulting in a shallow, reticulate population structure.

## MATERIALS AND METHODS

### Sampling Regime

Accurate estimates of population structure should be spatially comprehensive and collected over a relatively short interval (Waples & Gaggiotti 2006), particularly if the species in question could be capable of rapid large-scale movement (Wikelski et al. 2006). Published reports of mass *A. junius* movement show that consistent concentration zones occur in areas in which narrow projections of land such as barrier islands or

isthmuses are bounded by large bodies of water, such as estuaries, bays, the open ocean, or the North American Great Lakes, or extreme elevational shifts near large bodies of water (Lamborn 1890, Russell et al. 1998). Other consistent sites for southerly fall movement are south-pointing peninsulas, such as Point Pelee, Ontario, Canada, and Cape May, New Jersey, USA (Russell et al. 1998). All such concentration zones are also typical Neotropical bird migrant traps (Rappole 1995). Inland areas have lower densities of adult *A. junius* than coastal areas, and anecdotal evidence and personal observation suggest that inland areas may be more characterized by ranging or foraging behaviors than the focused and undistracted movement more typical of migration behavior generally (Dingle 1996). Sampling at 10 sites was conducted between 30 August and 17 October 2005 between Holiday Beach, Ontario, Canada (45° N latitude), along the Atlantic and Gulf coasts, and south to Chachalaca, Veracruz state, Mexico (19° N latitude; Figure 3–2). In order to include spring-emergent resident adults, we also collected 15 adults in early March 2006 in Austin, Texas (30°N latitude). All collection sites were wetlands near concentration zones. Adults were collected with an aerial net, sexed, and stored in glassine envelopes until tissue was placed in 100% ethanol. In total, 150 adults (N: 15 residents and 135 migrants) were captured, 24% of which were female, and 242 larvae, which were not sexed but were coded as spring- or fall-emergent (N: 176 residents and 41 migrants) larvae based on size class and time to emergence.


Figure 3–2. Collection sites for adult and larval *A. junius*.

**Microsatellite DNA Genotyping**

Nuclear microsatellite DNA, which consists of short tandem repetitive nucleotide sequences, has arguably become the gold standard of population genetic analysis given that these loci are diploid, codominant, and not under selection. Primers were developed for fourteen loci to enable population genetic analysis (Matthews et al. in press) though three loci showed poor amplification with this sample of individuals and two pairs of loci exhibited significant ($p<0.01$) linkage disequilibrium when analyzed via Genepop 3.2 (Raymond and Rousset 1995). Genepop 3.2 was also used to test Hardy-Weinberg Equilibrium (HWE) assumptions for the remaining nine loci. All 183 individuals used for genetic analysis were stored in 100% ethanol prior to extraction. DNA extraction, PCR, and analysis methods for these loci are as detailed in Matthews et al. (in press). Allelic diversity and observed vs. expected heterozygosity were calculated via GenAlEx 6.0 (Peakall & Smouse 2006).

Fst is a means of comparing between and within population genetic variance (Wright 1951, Cockerham & Weir 1987). Overall Fst and significance of pairwise Fst estimates were calculated using GenAlEx 6.0, using 1000 bootstrapped iterations. Pairwise Fst was also calculated for non-geographic groupings. For instance, the collection sites were treated as "populations," and the two sexes were treated likewise in a separate analysis. Pairwise matrices of geographic and genetic distance were also compared via a Mantel test to explore isolation-by-distance relationships (discussed by Weir 1996, Rouset 1997, and calculated using GenAlEx 6.0 via 100 iterations).

Microsatellite genotypes were also analyzed at the level of individuals rather than pre-defined populations. This procedure allowed testing for the optimal grouping of individuals into distinct reproductive units using Bayesian clustering methods (Pritchard et al. 2000, Gaggiotti et al. 2004). A central issue with such analytical approaches is selection of the most likely number of population clusters and individual assignment

within clusters (Waples & Gaggiotti 2006, Latch et al. 2006). Clustering was performed with two programs. The first, Structure 2.2 (Pritchard et al. 2000), requires post-processing to determine optimal clustering. Two major techniques have been used: selection based on rates of change in the variance of assignment likelihood averaged over multiple run iterations per level of population (*K*) (Evanno et al. 2005), and the mode of the posterior probability. A second, GESTE (Foll & Gaggiotti 2006), uses a hierarchical Bayesian approach that correlates pairwise Fst measurements with spatial variation in designated environmental variables, which in this case were latitude and longitude. Calculating the posterior likelihood, GESTE tests for the ability of selected variables, combinations of variables, coefficients, and combinations of coefficients and variables to explain the Fst variation.

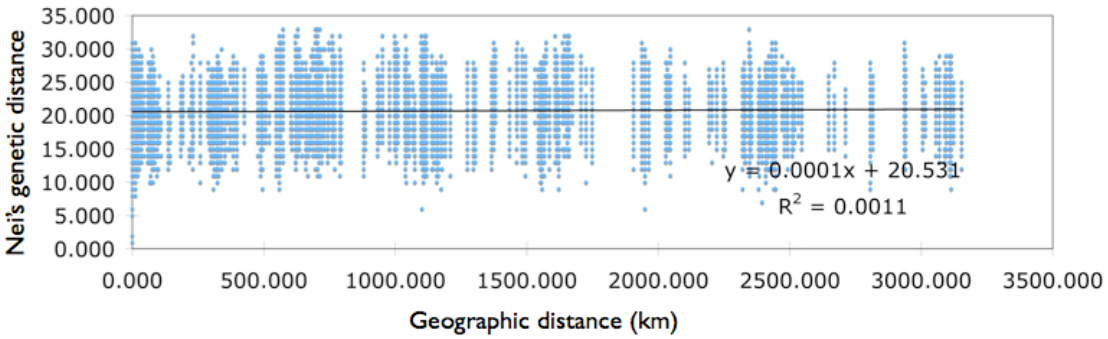


Figure 3–3. Mantel test comparing pairwise genetic and geographic distances for 242 larvae from 19 collection sites.

For larvae, we also examined kinship coefficients for individuals collected from a single wetland. Kinship coefficients (scaled from 0 to 1, with 1 being identical individuals) may not perform reliably without using dozens of microsatellite loci (Blouin 2003), but we selected two standard measures of kinship developed by Ritland (1996) and Wang (2002). All comparisons were made for larvae from each collection site.

## RESULTS

A Mantel test of the larvae showed no isolation by distance despite the use of individuals collected from localities up to 2600 km apart (Figure 3–3). Pairwise Fst estimates of these individuals range from 0.139 to <0.001 between individual populations, with a global estimate of 0.042 ($p < 0.001$) (Table 3–1). Only a handful of collection sites show significant deviations from HWE, and these only appear at a few loci. Average mean collection site heterozygosity (the difference between expected and observed heterozygosity) declines with latitude (range across loci, –0.153 to 0.264) (Figure 3–4).

Table 3–1. Pairwise Fst and Fst probabilities for larval *Anax junius,* showing collection latitude (degrees N latitude). Fst values below diagonal. Probability values based on 999 permutations are shown above diagonal. Probability values do not have a Bonferroni correction applied.

| 19.4 | 26.1 | 27.8 | 29.8 | 30.3 | 33.4 | 33.9 | 34.0 | 34.4 | 38.6 | 39.1 | 40.6 | 41.1 | 42.0 | 42.1 | 43.2 | 43.2 | 43.7 | 43.7 | 43.8 | 43.8 | 43.8 | 43.9 | 44.1 | 44.4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.000 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.010 | 0.006 | 0.012 | 0.001 | 0.001 | 0.001 | 0.001 | 0.014 | 0.001 | 0.001 | 0.001 | 0.007 | 0.001 | 0.013 | 0.001 | 0.022 | 0.119 |
| 0.055 | 0.000 | 0.001 | 0.001 | 0.001 | 0.029 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.004 | 0.001 |
| 0.022 | 0.093 | 0.000 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.009 | 0.012 | 0.013 | 0.001 | 0.001 | 0.001 | 0.002 | 0.031 | 0.003 | 0.028 | 0.004 | 0.048 | 0.001 | 0.029 | 0.014 | 0.107 | 0.291 |
| 0.024 | 0.095 | 0.017 | 0.000 | 0.001 | 0.001 | 0.001 | 0.046 | 0.002 | 0.001 | 0.010 | 0.001 | 0.001 | 0.001 | 0.001 | 0.198 | 0.001 | 0.020 | 0.001 | 0.008 | 0.001 | 0.184 | 0.001 | 0.344 | 0.413 |
| 0.055 | 0.130 | 0.065 | 0.067 | 0.000 | 0.001 | 0.001 | 0.001 | 0.001 | 0.018 | 0.040 | 0.002 | 0.001 | 0.001 | 0.004 | 0.047 | 0.001 | 0.009 | 0.001 | 0.047 | 0.001 | 0.001 | 0.001 | 0.021 | 0.009 |
| 0.049 | 0.032 | 0.070 | 0.071 | 0.097 | 0.000 | 0.001 | 0.001 | 0.001 | 0.003 | 0.114 | 0.001 | 0.094 | 0.001 | 0.002 | 0.015 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.004 | 0.001 | 0.004 | 0.002 |
| 0.059 | 0.094 | 0.064 | 0.061 | 0.072 | 0.091 | 0.000 | 0.001 | 0.001 | 0.002 | 0.015 | 0.002 | 0.001 | 0.001 | 0.002 | 0.043 | 0.001 | 0.014 | 0.003 | 0.025 | 0.001 | 0.003 | 0.001 | 0.071 | 0.004 |
| 0.019 | 0.076 | 0.024 | 0.007 | 0.062 | 0.060 | 0.040 | 0.000 | 0.001 | 0.002 | 0.063 | 0.001 | 0.001 | 0.134 | 0.001 | 0.054 | 0.043 | 0.059 | 0.009 | 0.023 | 0.011 | 0.291 | 0.003 | 0.130 | 0.453 |
| 0.017 | 0.088 | 0.019 | 0.018 | 0.075 | 0.065 | 0.083 | 0.022 | 0.000 | 0.015 | 0.118 | 0.006 | 0.001 | 0.043 | 0.001 | 0.087 | 0.001 | 0.015 | 0.001 | 0.006 | 0.008 | 0.010 | 0.083 | 0.217 | 0.395 |
| 0.030 | 0.098 | 0.032 | 0.042 | 0.056 | 0.055 | 0.084 | 0.046 | 0.030 | 0.000 | 0.117 | 0.001 | 0.001 | 0.001 | 0.026 | 0.094 | 0.001 | 0.013 | 0.008 | 0.093 | 0.007 | 0.037 | 0.031 | 0.111 | 0.097 |
| 0.041 | 0.096 | 0.044 | 0.033 | 0.065 | 0.030 | 0.086 | 0.027 | 0.022 | 0.037 | 0.000 | 0.075 | 0.006 | 0.061 | 0.011 | 0.078 | 0.015 | 0.230 | 0.019 | 0.015 | 0.049 | 0.304 | 0.064 | 0.169 | 0.050 |
| 0.057 | 0.118 | 0.062 | 0.040 | 0.103 | 0.103 | 0.098 | 0.042 | 0.036 | 0.078 | 0.036 | 0.000 | 0.001 | 0.012 | 0.004 | 0.058 | 0.001 | 0.050 | 0.001 | 0.007 | 0.001 | 0.005 | 0.006 | 0.029 | 0.006 |
| 0.061 | 0.064 | 0.085 | 0.071 | 0.115 | 0.019 | 0.086 | 0.064 | 0.090 | 0.072 | 0.078 | 0.107 | 0.000 | 0.001 | 0.004 | 0.028 | 0.001 | 0.001 | 0.002 | 0.005 | 0.002 | 0.001 | 0.001 | 0.002 | 0.001 |
| 0.030 | 0.082 | 0.035 | 0.016 | 0.084 | 0.068 | 0.079 | 0.006 | 0.012 | 0.050 | 0.027 | 0.027 | 0.076 | 0.000 | 0.001 | 0.113 | 0.001 | 0.013 | 0.001 | 0.004 | 0.022 | 0.067 | 0.019 | 0.128 | 0.186 |
| 0.066 | 0.172 | 0.070 | 0.076 | 0.135 | 0.114 | 0.139 | 0.096 | 0.084 | 0.078 | 0.134 | 0.109 | 0.099 | 0.082 | 0.000 | 0.394 | 0.001 | 0.006 | 0.003 | 0.022 | 0.003 | 0.001 | 0.001 | 0.054 | 0.005 |
| 0.050 | 0.131 | 0.042 | 0.015 | 0.083 | 0.075 | 0.080 | 0.039 | 0.035 | 0.063 | 0.066 | 0.064 | 0.065 | 0.027 | 0.008 | 0.000 | 0.031 | 0.159 | 0.079 | 0.235 | 0.209 | 0.072 | 0.066 | 0.483 | 0.294 |
| 0.030 | 0.100 | 0.028 | 0.025 | 0.083 | 0.065 | 0.066 | 0.014 | 0.050 | 0.060 | 0.048 | 0.084 | 0.091 | 0.038 | 0.099 | 0.048 | 0.000 | 0.012 | 0.002 | 0.122 | 0.013 | 0.166 | 0.001 | 0.071 | 0.473 |
| 0.038 | 0.094 | 0.026 | 0.021 | 0.074 | 0.066 | 0.054 | 0.019 | 0.032 | 0.052 | 0.019 | 0.041 | 0.078 | 0.030 | 0.093 | 0.035 | 0.038 | 0.000 | 0.024 | 0.091 | 0.059 | 0.061 | 0.080 | 0.197 | 0.039 |
| 0.028 | 0.098 | 0.026 | 0.026 | 0.085 | 0.058 | 0.065 | 0.021 | 0.030 | 0.041 | 0.052 | 0.051 | 0.066 | 0.030 | 0.078 | 0.041 | 0.036 | 0.022 | 0.000 | 0.008 | 0.048 | 0.130 | 0.012 | 0.021 | 0.118 |
| 0.059 | 0.158 | 0.047 | 0.053 | 0.086 | 0.117 | 0.104 | 0.054 | 0.068 | 0.063 | 0.107 | 0.106 | 0.135 | 0.077 | 0.138 | 0.051 | 0.034 | 0.053 | 0.072 | 0.000 | 0.010 | 0.029 | 0.021 | 0.053 | 0.196 |
| 0.028 | 0.071 | 0.026 | 0.015 | 0.089 | 0.040 | 0.057 | 0.015 | 0.022 | 0.038 | 0.035 | 0.059 | 0.044 | 0.014 | 0.074 | 0.018 | 0.022 | 0.021 | 0.014 | 0.075 | 0.000 | 0.114 | 0.044 | 0.445 | 0.120 |
| 0.021 | 0.077 | 0.020 | 0.006 | 0.074 | 0.049 | 0.073 | 0.005 | 0.023 | 0.032 | 0.010 | 0.050 | 0.059 | 0.015 | 0.106 | 0.047 | 0.010 | 0.026 | 0.012 | 0.055 | 0.012 | 0.000 | 0.129 | 0.080 | 0.476 |
| 0.022 | 0.085 | 0.014 | 0.018 | 0.071 | 0.059 | 0.076 | 0.023 | 0.010 | 0.024 | 0.028 | 0.035 | 0.055 | 0.014 | 0.057 | 0.033 | 0.038 | 0.016 | 0.016 | 0.054 | 0.012 | 0.010 | 0.000 | 0.086 | 0.112 |
| 0.046 | 0.111 | 0.027 | 0.006 | 0.095 | 0.099 | 0.059 | 0.021 | 0.020 | 0.049 | 0.047 | 0.066 | 0.109 | 0.026 | 0.092 | 0.000 | 0.044 | 0.030 | 0.060 | 0.111 | 0.000 | 0.041 | 0.033 | 0.000 | 0.438 |
| 0.013 | 0.092 | 0.006 | 0.001 | 0.071 | 0.060 | 0.068 | 0.000 | 0.003 | 0.026 | 0.038 | 0.051 | 0.080 | 0.010 | 0.094 | 0.018 | 0.000 | 0.034 | 0.016 | 0.026 | 0.013 | 0.000 | 0.014 | 0.003 | 0.000 |

Alternatively, the division of individual *A. junius* into two broad categories of spring- and fall-emergent groups is not reflected by a MANOVA, even when these distinctions are broken down further into presumably more uniform adult and larval life stages (Table 3–2). Observed heterozygosity ($H_o$) tends to be slightly lower than expected in all four categories (range of difference, $H_e - H_o$, 0.035 to 0.180). All but one locus within each three of the categories (fall-emergent migrant adults and both fall- and spring-emergent larvae) are out of HWE ($p<0.01$). The spring-emergent adults represent the smallest sample size and lowest population site diversity; they show 7 loci in HWE and 2 out of HWE ($p<0.01$). They represent collection over a brief period of days at a single site. Presumably a larger sample collected during this period would match the other three categories.

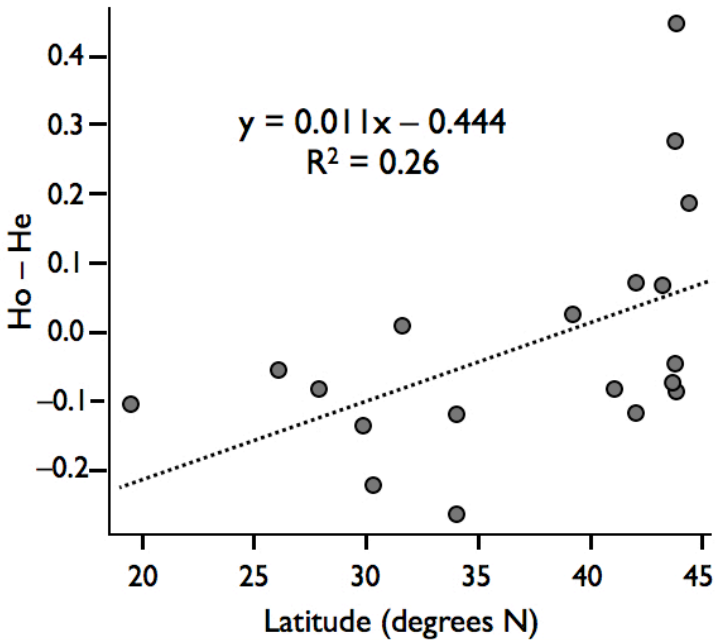


Figure 3–4. The relationship between the difference in observed and expected heterozygosity across latitude.

| Adult fall-emergent migrants | Adult spring-emergent residents | Larval fall-emergent migrants | Larval spring-emergent residents | |
|---|---|---|---|---|
| | 0.001 | 0.001 | 0.001 | **Adult fall-emergent** |
| 0.023 | | 0.002 | 0.001 | **Adult spring-emergent** |
| 0.006 | 0.017 | | 0.011 | **Larval fall-emergent** |
| 0.009 | 0.022 | 0.003 | | **Larval spring-emergent** |

Table 3–2. MANOVA of *Anax junius* categories based on 9 microsatellite loci across 367 individuals: adults, larvae, residents (spring-emergent), and migrants (fall-emergent). Fst values below diagonal. Probability values based on 999 permutations are shown above diagonal.

The Bayesian techniques produced roughly comparable results though they use quite different methodologies. GESTE found that a model using latitude had an 11% likelihood, while longitude had a 12% likelihood (Figure 3–5). A model combining latitude and longitude had a 1% likelihood.

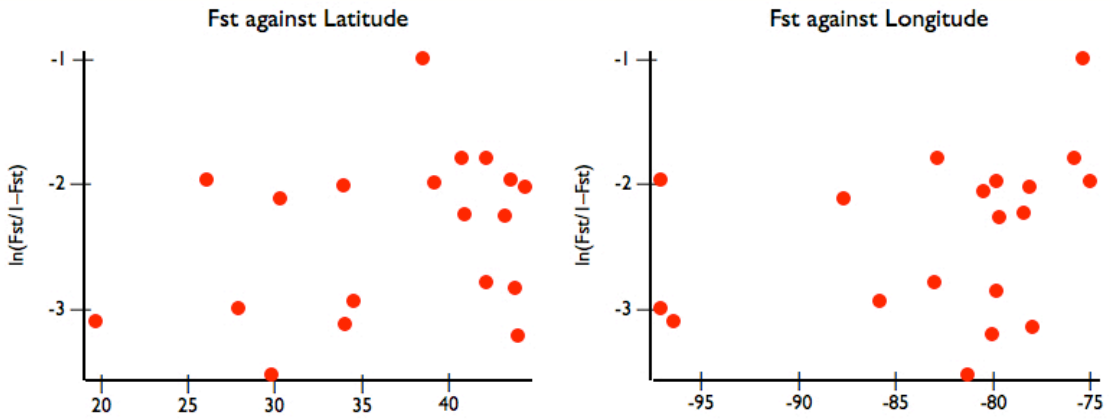


Figure 3–5. The relationship between Fst and latitude (left) and longitude (right), as estimated by GESTE, showing the posterior probability for the relationship between Fst at 19 larval collection sites and latitude (posterior probability = 11%) and longitude (posterior probability = 12%).

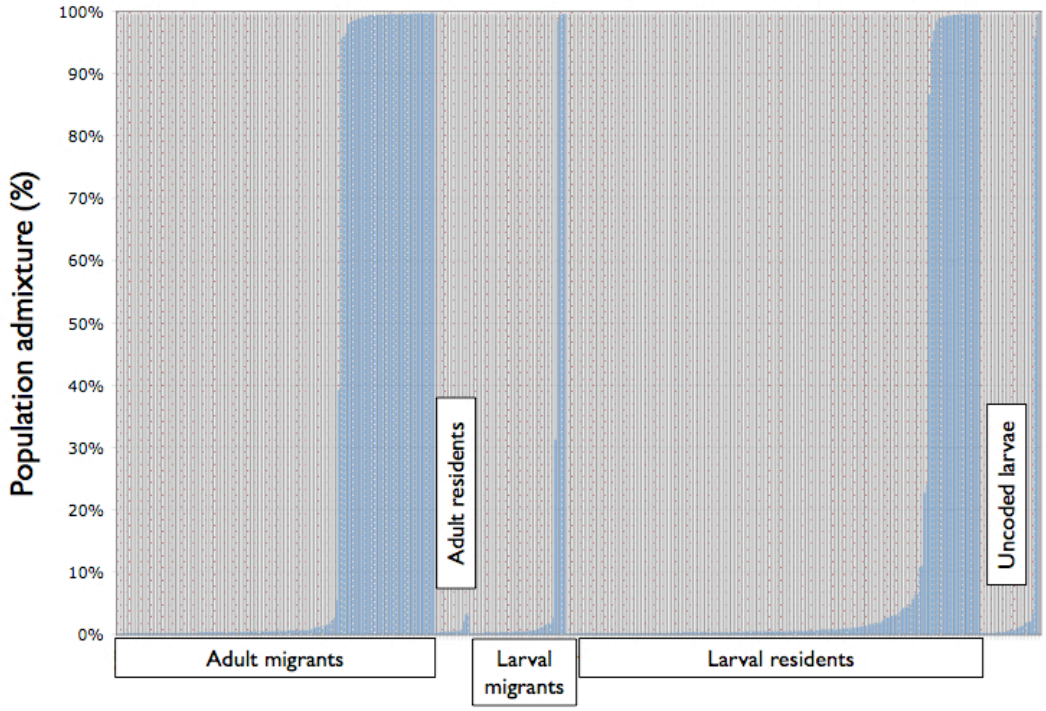


Figure 3–6. Two-population solution for population admixture, sorted by relative population 1 membership within each life-stage category.

Optimal clustering in Structure without regard to *a priori* assumptions about life stage or collection site generates similar patterns (Table 3–3). Posterior probability model selection chooses 15 populations (K) as the optimal model based on all individuals ($p>0.99$), while an analysis of rates of change in likelihood ($\Delta K$, after Evanno et al. 2005) selected 19 populations for the larvae, 1 for the adults, and 2 for all individuals. A similar analysis comparing spring-emergent residents and fall-emergent migrants had a mode of the posterior likelihood over 20 iterations of 15 populations (K), with a $\Delta K$ for residents of 14, migrants of 2, and all individuals of 2 (Table 3–4). At any given level of K, Structure determines the relative membership or admixture of each individual with the constituent levels of K. Thus, a single individual may be wholly or partially a member of one population at a given value of K, and partial membership may be spread across

multiple values of K. Constituent membership for the 2-population solution with all individuals is shown in Figure 3–6, and ΔK variation over K values from 1 to 20 are shown in Figure 3–7. All but six members showed less than 10% admixture.

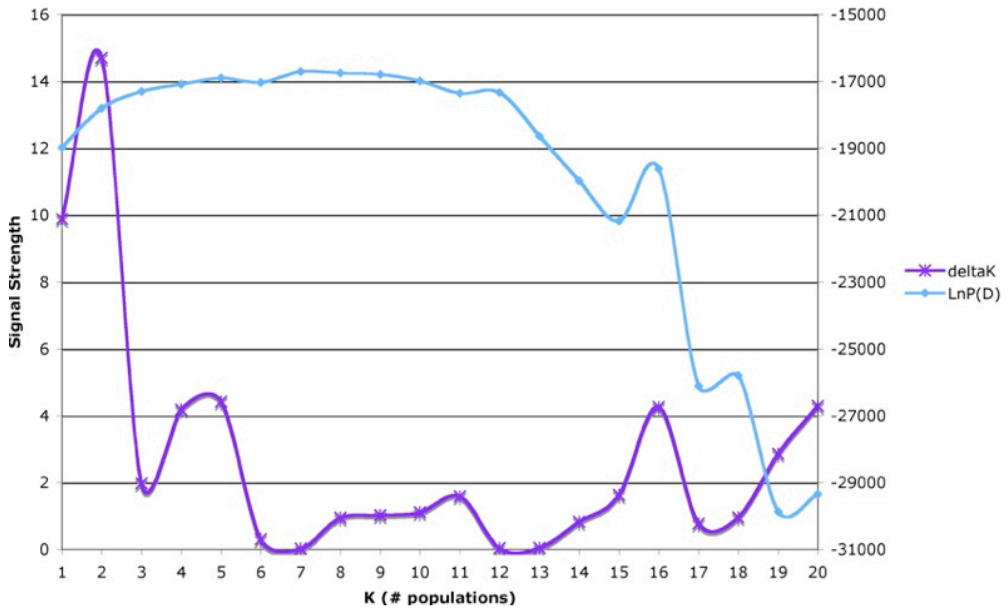


Figure 3–7. Variation in mean clustering (K) values (averaged 20 iterations/K) and LnP(D) over K from 1 through 20. Based on Pritchard et al. (2000) and Evanno et al. (2005).

| **Life stage (K1–20)** | **N** | **ΔK 1° peak** | **ΔK 2° peak** | **Posterior[1]** |
|---|---|---|---|---|
| Larvae | 242 | 19 | 16 | 20 (p>.99) |
| Adults | 150 | 1 | 15 | 15 (p>.99) |
| All individuals | 392 | 2 | 5 | 15 (p>.99) |

[1] Determined using both the mean ln(likelihood) by K (averaged over 20 iterations/K) and the variance in ln(likelihood) by K (also averaged over 20 iterations/K).

Table 3–3. A range of optimal peaks for adult and larval *A. junius*, based on clustering analysis of Structure data.

| Emergence Group (K1–20) | N | ΔK 1° peak | ΔK 2° peak | Posterior[1] |
|---|---|---|---|---|
| Spring (residents) | 191 | 14 | 5 | 11 (p>.99) |
| Fall (migrants) | 176 | 2 | 13 | 10 (p>.99) |
| All individuals | 392 | 2 | 5 | 15 (p>.99) |

[1] Determined using both the mean ln(likelihood) by K (averaged over 20 iterations/K) and the variance in ln(likelihood) by K (also averaged over 20 iterations/K).

Table 3–4. A range of optimal peaks for spring- and fall-emergent *A. junius*, based on clustering analysis of Structure data.

A logistic regression of all individuals from the 2-population solution found that degree of population membership was best explained as a function of life stage/emergence group ($p<0.01$, excluding uncoded larvae and resident adults, of which the latter came from a single site), latitude ($p<0.001$), and longitude ($p<0.01$). This model had the lowest AIC value (289) and significance ($p<0.001$) with an $R^2$ of 0.12. Though significant, the effect of each variable was small ($0.1 < 0.009$). Model dispersion was low, with a residual deviance of 45 compared to 347 degrees of freedom. Stepwise AIC value comparison for all combinations of variables showed the complete model had the best fit ($p<0.001$).

Intra-collection site relatedness was quite low (Tables 3–5 and 3–6) despite using nine polymorphic loci and, for analytical purposes, negligible. Using the Ritland (1996) method, mean relatedness over 19 collection sites was only 0.05 within a single pond ($1\sigma$: 0.05). Wang's (2002) more recent method of estimating relatedness is more conservative (Blouin 2003), with a mean of –0.04 ($1\sigma$: 0.03); negative values reflect sampling error.

Table 3–5. Intra-pond kinship coefficients following Ritland (1996).

| **N** | 17 | 36 | 15 | 7 | 6 | 7 | 16 | 17 | 11 |
|---|---|---|---|---|---|---|---|---|---|
| **site** | **Chach, MX** | **St Aug, Fl** | **Port Aransas, Tx** | **S Padre, Tx** | **Gulf Shores, AL** | **Bitter Lake, NM** | **Cape Fear, NC** | **Wilgtn, NC** | **Dogtown, AL** |
| **latitude** | 19.8 | 29.8 | 27.8 | 26.1 | 30.3 | 33.4 | 33.9 | 34 | 33.4 |
| **overall R** | 0.08 | 0.11 | 0.07 | 0.02 | 0.12 | 0.02 | 0.12 | 0.10 | 0.04 |
| ***loci*** | | | | | | | | | |
| **a** | 0.10 | 0.08 | -0.05 | -0.07 | 0.25 | 0.00 | 0.20 | 0.13 | -0.07 |
| **b** | 0.06 | 0.02 | -0.09 | 0.13 | 0.14 | 0.06 | -0.01 | 0.09 | 0.04 |
| **c** | 0.24 | 0.30 | 0.07 | 0.47 | 0.11 | 0.00 | 0.19 | 0.15 | 0.17 |
| **d** | 0.03 | 0.08 | 0.06 | | 0.33 | | -0.03 | 0.03 | -0.04 |
| **e** | 0.03 | 0.11 | 0.14 | -0.06 | 0.09 | 0.03 | 0.02 | 0.05 | -0.13 |
| **f** | 0.20 | 0.20 | 0.02 | 0.06 | 0.00 | 0.02 | 1.00 | 0.29 | 0.04 |
| **g** | 0.00 | 0.13 | 0.25 | -0.09 | 0.14 | 0.19 | 0.16 | -0.04 | 0.04 |
| **h** | 0.03 | -0.02 | 0.15 | 0.06 | 0.17 | 0.00 | 0.12 | 0.16 | 0.20 |
| **i** | 0.06 | 0.04 | -0.14 | -0.08 | -0.10 | -0.04 | 0.16 | 0.05 | 0.00 |
| **N** | 6 | 8 | 7 | 14 | 15 | 8 | 14 | 6 | 10 |
| **site** | **central PA** | **Eastern PA** | **Niagara Penn, ON** | **Holiday Beach, ON** | **Creemore Sprgs, ON** | **Orangevile, ON** | **Claude, ON** | **Creon, ON** | **Kilkinney, ON** |
| **latitude** | 40.6 | 41.1 | 33.4 | 42 | 43.8 | 43.8 | 43.876 | 44.4 | 43.7 |
| **overall R** | 0.03 | 0.00 | 0.02 | 0.08 | 0.05 | -0.01 | 0.09 | -0.06 | 0.06 |
| ***loci*** | | | | | | | | | |
| **a** | -0.17 | -0.08 | 0.00 | 0.04 | 0.00 | 0.00 | 0.02 | -0.14 | 0.00 |
| **b** | -0.14 | -0.11 | 0.06 | 0.00 | 0.08 | 0.00 | 0.11 | -0.17 | 0.03 |
| **c** | -0.13 | 0.33 | 0.00 | 0.09 | -0.05 | 0.07 | 0.08 | 0.00 | -0.08 |
| **d** | 0.50 | 0.00 | | 0.30 | 0.30 | -0.06 | 0.23 | 0.10 | 0.37 |
| **e** | 0.24 | -0.02 | 0.03 | 0.04 | 0.23 | -0.13 | 0.11 | -0.20 | -0.06 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **f** | -0.08 | 0.20 | 0.02 | 0.16 | 0.10 | 0.13 | 0.05 | 0.17 | 0.08 |
| **g** | 0.13 | -0.03 | 0.19 | 0.04 | 0.07 | -0.04 | 0.19 | -0.13 | -0.04 |
| **h** | 0.00 | -0.23 | 0.00 | 0.31 | -0.05 | 0.00 | 0.04 | 0.08 | 0.07 |
| **i** | -0.25 | 0.20 | -0.04 | -0.10 | -0.10 | 0.13 | -0.08 | -0.13 | 0.48 |

Table 3–6. Intra-pond kinship coefficients following Wang (2002).

| **N** | 17 | 36 | 15 | 7 | 6 | 7 | 16 | 17 | 11 |
|---|---|---|---|---|---|---|---|---|---|
| **site** | **Chach, MX** | **St Aug, Fl** | **Port Ar, Tx** | **S Padre, Tx** | **Gulf Sh, AL** | **Bitter Lk, NM** | **Cape Fr, NC** | **Wilm, NC** | **Dogtown, AL** |
| **latitude** | 19.8 | 29.8 | 27.8 | 26.1 | 30.3 | 33.4 | 33.9 | 34 | 33.4 |
| **overall R** | 0.01 | -0.02 | -0.03 | -0.03 | -0.12 | -0.02 | -0.12 | -0.02 | -0.03 |
| ***loci*** | | | | | | | | | |
| **a** | 0.00 | -0.01 | -0.02 | -0.05 | -0.14 | 0.05 | -0.28 | 0.00 | 0.00 |
| **b** | 0.01 | 0.00 | 0.02 | 0.00 | -0.06 | 0.01 | -0.02 | -0.01 | -0.02 |
| **c** | 0.05 | -0.03 | -0.02 | 0.00 | -0.10 | 0.00 | -0.05 | -0.03 | -0.11 |
| **d** | 0.07 | -0.05 | -0.06 | | -0.07 | | -0.05 | 0.01 | -0.05 |
| **e** | 0.00 | -0.02 | -0.02 | -0.04 | -0.23 | -0.03 | -0.19 | -0.01 | 0.03 |
| **f** | 0.07 | -0.13 | 0.00 | -0.19 | -0.10 | 0.02 | -0.74 | -0.16 | -0.09 |
| **g** | 0.02 | -0.01 | -0.06 | 0.00 | 0.00 | -0.04 | -0.10 | 0.00 | -0.01 |
| **h** | -0.01 | 0.00 | -0.08 | 0.02 | -0.38 | -0.04 | -0.11 | -0.07 | -0.04 |
| **i** | 0.01 | -0.02 | 0.07 | 0.00 | 0.00 | -0.07 | -0.12 | -0.02 | -0.03 |

| **N** | 6 | 8 | 7 | 14 | 15 | 8 | 14 | 6 | 10 |
|---|---|---|---|---|---|---|---|---|---|
| **site** | **central PA** | **Eastern PA** | **Niag pen, ON** | **HldyBch, ON** | **Cr Sprgs, ON** | **Oville, ON** | **Claude, ON** | **Creon, ON** | **Kilkinny, ON** |
| **latitude** | 40.6 | 41.1 | 43.2 | 42 | 43.8 | 43.8111 | 43.876 | 44.4 | 43.7 |
| **overall R** | -0.04 | -0.02 | -0.03 | -0.04 | -0.03 | -0.04 | -0.03 | 0.00 | -0.05 |
| ***loci*** | | | | | | | | | |
| **a** | 0.06 | 0.00 | -0.01 | -0.02 | -0.01 | 0.00 | -0.01 | 0.03 | -0.01 |
| **b** | -0.01 | 0.00 | -0.01 | 0.00 | -0.02 | 0.00 | -0.02 | 0.00 | -0.03 |
| **c** | 0.00 | -0.20 | -0.02 | -0.09 | -0.01 | -0.10 | -0.02 | -0.05 | -0.05 |
| **d** | -0.13 | -0.06 | -0.01 | -0.07 | -0.05 | -0.01 | -0.05 | -0.01 | -0.28 |
| **e** | -0.08 | -0.01 | -0.01 | -0.01 | -0.06 | -0.01 | 0.00 | 0.00 | 0.00 |
| **f** | -0.02 | -0.28 | -0.06 | -0.32 | -0.34 | -0.26 | -0.16 | 0.02 | -0.15 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **g** | -0.16 | -0.02 | -0.06 | -0.02 | -0.01 | -0.01 | -0.03 | 0.02 | 0.00 |
| **h** | 0.40 | 0.37 | -0.01 | -0.05 | 0.04 | -0.02 | -0.03 | 0.00 | -0.10 |
| **i** | -0.01 | -0.02 | -0.01 | 0.01 | 0.15 | -0.15 | 0.08 | | -0.25 |

## DISCUSSION

Across eastern North America, *A. junius* population structure form a low number of spatially intermingled units, effectively forming a single population. The global Fst value for *A. junius* is striking for its low level, with just 4% of variation explained by inter–collection site differences. Weak clinal patterns in heterozygosity and genotype extend across the continent, but the phylogeography of *A. junius* seems relatively continuous, uninterrupted by mountains, Great lakes, rivers, and even the Gulf of Mexico.

Relatively uniform patterns of gene flow are unusual over large scales and typically occur in species in which high rates of dispersal jumble populations and genes. Many of the best-documented examples are marine species (Palumbi 1994). While not as low as European eel *Anguila anguila* with Fst levels (~0.001; Wirth & Bernatchez 2001), *A. junius* Fst levels are higher than those migratory salmon (~0.10; Wenburg et al, 1998). Unfortunately, many of the terrestrial species most comparable to *A. junius* in terrestrial patterns — particularly migratory Lepidoptera (butterflies and moths) — have either not been studied for large-scale phylogeographic patterns or they have proven resistant to analysis with fine-scaled molecular markers such as microsatellites (Zhang 2004).

Birds are another natural source of comparison with *A. junius* patterns. However, avian microsatellite phylogeography has surprisingly lagged behind many other vagile taxa (Crochet 2000, Wink 2005), and many avian phylogeography studies are conducted as conservation genetics research on endangered or threatened species, which may also lend a bias to these studies. Given that caveat, in a review comparing Fst accuracy across a variety of molecular markers, Crochet (2000) summarized a range of passerine global Fst values spanning a high of 0.16 (from Piertney et al. 1998) to 0.009 (from Dias et al. 1996). Taken together, highly vagile species from both marine and terrestrial safely bound the global Fst values seen in *A. junius*.

Low rates of dispersal can be associated with species showing high rates of gene flow, though there are few examples of these patterns. For instance, unusual meteorological conditions temporarily altered the distribution of critical resources for turbot (*Psetta maxima*) throughout the Baltic Sea, leading normally sessile eggs and adults to become widely admixed and reducing Fst (e.g., Florin & Höglund 2007). However, there is no reason to believe that the patterns we see here with *A. junius* represent an unusual year.

**Selection of the Optimal Number of Eastern North American Populations and Intra-pond Relatedness**

With the low global Fst value and one effective eastern population, discussion falls to what explains the small amount of spatial variation detected and if *A. junius* are best described as falling into either a handful of meaningful reproductive units (~1 to 2) or many (~15 to 19).

The larvae appear to be structured primarily by collection site (K = 19; Table 3–3) but, as the kinship coefficients for collection sites demonstrate, even the levels of relatedness within collection sites are low, roughly corresponding in the case of Ritland's (1996) coefficient of relatedness to the mean global Fst.

What spatial component that does exist in *A. junius* may be limited to larval sibling groups within single wetlands or small groups of nearby wetlands, patterns that are largely erased after a single generation or bivoltine cycle as these individuals emerge and disperse across the landscape. Intra-pond relatedness estimates probably suffer from low power, but the general pattern also seems clear: single ponds contain larvae resulting from many parents and are thus characterized as assemblages of mostly unrelated or distantly related individuals. The combination of highly polymorphic loci, relatively low numbers of individuals per site (mean: 12.3), and nine loci weaken the analytical basis of

kinship estimates. Even with these constraints and caveats, however, it is clear that each pond is a allelic soup of individuals. Iteroparous mating likely plays a major role here. Males typically guard some portion of the shoreline waiting for females to arrive (Buskirk & Sherman 1985), which should at least imply that each pond would reflect a limited number of paternal contributions and thus many half-sibs. Moreover, while damselflies (Odonata: suborder Zygoptera) are well known for the ability of females to store sperm from multiple males, this behavior is much less known in dragonflies (Odonata: suborder Anisoptera), primarily for lack of study rather than the belief that this behavior occurs (reviewed in Corbet 1999). If female *A. junius* can store sperm from previous matings, then the number of half-sibs may be further diminished. Clearly more systematic work on the reproductive and mating strategies of male and female *A. junius* is necessary to clarify these issues.

Most reviewers of the algorithms used in Bayesian clustering programs like Structure reject the use of the posterior likelihood as a determinant of optimal K, and interpretation of the Structure-generated optimal clustering for each category of *A. junius* can be complex. When a ΔK analysis is made and a variety of potential solutions are presented by the same data set, the assumption is to parsimoniously defer to smaller *K* models (Pritchard 2000, Evanno et al. 2005, Manel et al. 2005, Waples & Gaggiotti 2006), particularly when global Fst levels are 0.05 or below (Latch et al. 2006), which clearly applies to this case. The larvae appear to be structured primarily by collection site (K = 19), while the adults and all individuals show far lower numbers of constituent groups (K = 2 and 1, respectively); analysis of these groups shows extremely weak spatial relationships (coefficients ~0.01) for the adult population membership. Folding the adults and larvae into a single group must wash out the larval collection-site signals from the ability of Structure to detect. Likewise, the presence of two emergence groups

by itself also seems to be a poor means of explaining the small amount of spatial observation.

That said, the lack of larval population structure does allow some room for inference about the nature of that movement during the adult stage. Perhaps the strongest conclusion is that migration by *A. junius* adults is reproductive movement, with the evidence of egglaying and mating written over the landscape. Moreover, the minimal structure reflected by the pairwise Fst values (Table 3–1) suggests that not all large-scale movement is southbound by adults. Strictly southbound movement would create a clinal pattern of gene flow, with genetic diversity declining from south to north as genotypes are bled off of northern regions. In fact, observed heterozygosity tends to increase with latitude. Northern movement may be an even more significant source of genetic diversity than southern migration. While strong proxy evidence and almost a century of anecdotes show fall movement by adults, the molecular evidence alone does not rule out movement in other directions during the fall and/or a spring migration (Soltesz et al. 1995, Russell et al. 1998).

Our findings that rapid rates of gene flow are occurring over North America represent significant evidence that *A. junius* is capable of intra-generational large-scale dispersal, and that this movement has strong population genetic inter-generational implications. We believe that these patterns point to the need to conduct additional studies on other purported insect migrants, and that these results should serve as an important benchmark for comparison.

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## LITERATURE CITED

Artiss, T. 2004. Phylogeography of a facultatively migratory dragonfly, *Libellula quadrimaculata* (Odonata: Anisoptera). *Hydrobiologia* 515, 225–234.

Avise, J.C., 2000. *Phylogeography: the history and formation of species*. Cambridge, MA: Harvard University Press.

Bilton, D.T., J. R. Freeland, and Okamura. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32, 159–181.

Blouin, M.S. 2003. DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends in Ecology and Evolution* 18(10), 503–511.

Bowen G. J., L. I. Wassenaar, and K.A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* **143**, 337-348.

Buskirk, R.E., and K.J. Sherman. 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Florida Entomology* 68(1), 39–51.

Catling, P. 2004. *Anax junius* overwintering in eastern Ontario. *Ontario Odonata* 5: 12–15.

Chapuis, M.P., and A. Estoup. In press. Microsatellite null alleles and estimation of population differentiation. *Molecular Biology and Evolution*

Cockerham, C.C., and B.S. Weir. 1987. Correlations, descent measures: drift with migration and mutation. *Proceedings of the National Academy of Sciences* 84(23), 8512–8514.

Cole, L.C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29(2), 103–137.

Corbet, P.S. 1999. *Dragonflies: behavior and ecology of Odonata*. Ithaca: Cornell University Press.

Crochet, P.-A. 2000. Genetic structure of avian populations—allozymes revisited. 2000. *Molecular Ecology* 9, 1463–1469.

Dias, P.C., G.R. Verheyen, and M. Raymond. 1996. Source-sink populations in Mediterranean Blue tits: evidence using single-locus minisatellite probes. *Journal of Evolutionary Biology* 9, 965–978.

Dingle, H. 1996. *Migration: the biology of life on the move*. New York: Oxford University Press.

Dudley, R. 2000. *The biomechanics of insect flight*. Princeton, NJ: Princeton University Press.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software Structure: a simulation study. *Molecular Ecology* 14(8), 2611–2620.

Florin, A.B., and J. Höglund. 2007. Absence of population structure of turbot (*Psetta maxima*) in the Baltic Sea. *Molecular Ecology* 16, 115–126.

Foll, M., and O. Gaggiotti. 2006. Identifying the environmental factors that determine the genetic structure of populations. *Genetics* 174, 875–891.

Freeland, J., M. May, R. Lodge, and K.F. Conrad. 2003. Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner *Anax junius*. *Ecological Entomology* 28, 413–421.

Funk, C., T. Mullins, and S. Haig. In press. Conservation genetics of snowy plovers (*Charadrius alexandrinus*) in the western hemisphere: population genetic structure and delineation of subspecies. *Conservation Genetics*

Gaggiotti, O., S.P. Brooks, W. Amos, and J. Harwood. 2004. Combining demographic, environmental and genetic data to test hypotheses about colonization events in metapopulations. *Molecular Ecology* 13(4), 811–825.

Hanski, I., C. Erlahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7(10), 958–966.

Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25, 167–188.

Kenchington, E., M. Patwary, R. Zouros, and C. Bird. 2006. Genetic differentiation in relation to marine landscape in a broadcast-spawning bivalve mollusc (*Placopecten magellanicus*). *Molecular Ecology* 15, 1781–1796.

Lamborn, R.H. (ed). 1890. *Dragonflies vs. mosquitoes*. New York: D. Appleton & Co.

Latch, E.K., G. Dharmarajan, J.C. Glaubitz, and O.E. Rhodes. 2006. Relative performance of Bayesian clustering software for inferring substructure and individual assignment at low levels of population differentiation. *Conservation Genetics* 7, 295–302.

Lessios, H.A., and C.W. Cunningham. 1984. Gametic incompatibility between species of the sea urchin *Echinometra* on the two sides of the isthmus of Panama. *Evolution* 44(4), 933–941.

Manel, S., O. Gaggiotti, and R. Waples. 2005. Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution* 20, 136–142.

Matthews, J.H. 2004. Shifts in common green darner emergence patterns? *Ontario Odonata* 5: 12–15.

Matthews, J.H., S. Boles, C. Parmesan, and T. Juenger. In press. Isolation and characterization of nuclear microsatellite loci for the common green darner dragonfly *Anax junius* (Odonata: Aeshnidae) to constrain patterns of phenotypic and spatial diversity. *Molecular Ecology Notes*

Needham, J.G., M.J. Westfall, and M. May. 2000. *Dragonflies of North America*. Gainesville, FL: Scientific Publishers.

Palumbi, S.R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* 25, 547–572.

Pascarella, J.B. 2007. Mechanisms of prezygotic reproductive isolation between two sympatric species, *Gelsemium rankinii* and *G. sempervirens* (Gelsemiaceae), in the southeastern United States. *American Journal of Botany* 94, 468–476.

Paulson, D.R. 1966. Dragonflies (Odonata: Anisoptera) of South Florida. Ph.D. Dissertation, University of Miami, 603 pp.

Peakall, R., and P.E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Popuation genetic software for teaching and research. *Molecular Ecology Notes* (6(1), 288–295.

Piertney SB, MacColl ADC, Bacon PJ, Dallas JF (1998) Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. *Molecular Ecology*, 7, 1645–1654.

Pritchard, J.K., M. Stephens, and P. J. Donnelly, 2000. Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959.

Rankin, M. A., McAnelly, M. L., Bodenhamer, J. E. 1986. The oogenesis-flight syndrome revisted. In *Insect flight: Dispersal and migration*, ed. W. Danthanarrayana. pp. 27-48. Heidelberg and Berlin: Springer-Verlag.

Rappole, J.H. 1995. *The ecology of migrant birds: a Neotropical perspective*. Washington, DC: Smithsonian Institution Press.

Raymond, M., and F. Rousset. 1995. GENEPOP: population genetics software for exact tests and ecumenism. *Journal of Heredity* 86(3): 248–49.

Ritland, K. 1996. A marker-based method for inferences about quantitative inheritance in natural populations. *Evolution* 50(3), 1062–1073.

Rouquette, J.R., and D. Thompson. 2007. Roosting site selection in the endangered damselfly *Coenagrion mercuriale,* and implications for habitat design. *Journal of Insect Conservation* 2, 187–193.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145:1219-1228.

Russell, R.W. 2005. *Interactions between migrating birds and offshore oil and gas platforms in the northern Gulf of Mexico: Final Report*. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2005-009.

Russell, R.W., M.L. May, K.L. Soltesz, and J.W. Fitzpatrick. 1998. Massive swarm migrations of dragonflies in eastern North America. *American Midlands Naturalist* 140(2), 325–342.

Soltesz, K., B. Barber, and G. Carpenter. 1995. A spring dragonfly migration in the Northeast. *Argia* 7(3):10-14.

Trottier, R. 1970. Effect of temperature and humidity on emergence in *Anax junius*. Ph.D. Dissertation, University of Toronto, Toronto, Ontario.

Trottier, R. 1971. Effect of temperature on the life-cycle of *Anax junius* in Canada. *Journal of Canadian Entomology* 103, 1671–83.

Walker, E.M. 1958. *The Odonata of Canada and Alaska*. Vol. 2. Toronto, Canada: University of Toronto Press.

Wang, J. 2002. An estimator of pairwise relatedness using molecular markers. *Genetics* 160, 1203–1215.

Waples, R.S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for evaluating the number of gene pools and their degree of connectivity. *Molecular Ecology* 15(6), 1419–1439.

Wenburg, J., P. Bentzen, and C. Foote. 1998. Microsatellite analysis of genetic population structure in an endangered salmonid: the coastal cutthroat trout (*Oncorhynchus clarki clarki*). *Molecular Ecology* 7, 733–749.

Wikelski, M., D. Moskowitz, J.S. Adelman, J. Cochrain, D.S. Wilcove, and M.L. May. 2006. Simple rules guide dragonfly migration. *Biology Letters* 2(3), 325–329.

Williams, C.B. 1957. Insect migration. *Annual Review of Entomology* 2, 163–180.

Wirth, T., and L. Bernatchez. 2001. Genetic evidence against panmixia in the European eel. *Nature* 409(6823), 1037–1040.

Wink, M. 2005. Use of DNA markers to study bird migration. *Journal of Ornithology* 147(2), 234–244.

Wissinger, S.A. 1988. Life history and size structure of larval dragonfly populations. *Journal of the North American Benthic Society* 7, 13-28.

Wright, S. The genetical structure of populations. *Annals of Eugenics* 15, 323–354.

Zhang, D. 2004. Lepidopteran microsatellite DNA: redundant but promising. *Trends in Ecology and Evolution* 19, 507–509.

# Chapter 4

## Larval Photoperiod Regime Determines Adult Movement Strategy in a Migratory Dragonfly, *Anax junius* Drury (Odonata: Aeshnidae)[1]


**ABSTRACT**

In species with multiple distinct developmental trajectories members of the same population may choose different tactics and develop different behavioral or physical phenotypes. Such differences can be based on heritable variation and/or on plastic responses to environmental cues. Species whose ranges extend over large latitudinal gradients and that exhibit high rates of inter-population gene flow in particular face barriers to local adaptation in life-history pattern. When such species also show multiple developmental tactics it may be difficult for them to evolve different ways of triggering those developmental patterns in different habitats. In consequence they are likely to follow reliable ambient cues that operate across the full geographical range, if such cues exist. *Anax junius* is a widespread North American dragonfly species that shows two distinct larval life-history trajectories over its full range. These two trajectories are also associated with distinct adult large-scale movement patterns. Here we test the hypothesis that changing photoperiod can trigger alternate developmental pathways in larval dragonflies, resulting in distinct adult movement strategies. Using a split-sibling common-garden experimental design, we exposed larvae to increasing, decreasing, or constant photoperiods for two months from the time of oviposition. Increasing (spring)


[1] Camille Parmesan, Morgan Kelly, and Thomas Juenger were significant collaborators on this chapter.

photoperiods caused significantly faster larval growth rates than decreasing (fall) and constant (control) photoperiods. These different developmental rates are associated with different adult movement tactics: fast-growing larvae become south-bound fall migrants, while slower larvae become sedentary adults. Our results therefore support the hypothesis that developmental pathway and adult movement strategies are regulated by larval exposure to spring vs. fall photoperiods.

## INTRODUCTION

The timing of major life-history events and processes can be cued and constrained by mechanisms operating both within and external to an individual organism. With poikilothermic organisms such as insects, extra-organismal forces play an especially strong role in determining the timing of life-history events since internal states are necessarily responsive to environmental conditions. In many cases, ambient conditions impact life-history timing in relatively minor ways. For instance, an especially cold morning may induce a delay in the onset of emergence of a few hours or a day (Trottier 1970).

Environmental cues may also serve to signal more sweeping changes in life-history timing, developmental pathways, and larval and adult phenotype. These aspects of life-history phenology are referred to as "regulated development" by Corbet (1999) to distinguish their influence from both small adjustments in timing as well as life-history patterns that appear unfettered by environmental cues, as is seen in some tropical insect species. In contrast, seasonality is a common attribute of insect development in temperate zones, suggesting some regulatory interaction between life-history pattern and environmental signals. For instance, a shrinking pond may cue more rapid larval development to avoid dry conditions (De Block and Stoks 2005), photoperiod can trigger

diapause (Boivin et al. 2004), or low temperatures might induce a distinct wing morphology (Bégin et al. 2004).

Associations between seasonal variation in environmental factors and broad types of life-history patterns have long been invoked with odonates (dragonflies and damselflies), an ancient order of insects with a generally aquatic larval stage and terrestrial adult stage. Corbet and Corbet (1958) described two major life-history patterns seen in temperate latitudes: a "spring" or type-1 (T1) pattern whose larvae overwinter in the final larval instar and emerge as adults in early spring, and a "summer" or type-2 (T2) pattern that overwinter in a non-final instar and emerge in late spring, summer, or early fall. Later, a third category — type-3 or T3 pattern — was described by Corbet (1960), characterized as univoltine and overwintering as an egg or being oviposited in spring and emerging during the summer or fall (summarized in Corbet 1999, 2003). More than one pattern may be seen in a single odonate species. For instance, within a single pond, there may be T1 and T2 *Anax imperator* individuals (Corbet 1957). Across large altitudinal, longitudinal, or latitudinal gradients, there may also be shifts within a species, as from T3 at low or subtropical latitudes to T2 at high latitudes (Corbet 2003).

The mechanisms that determine life-history timing differences within and between odonate species have proven to be complex and, to date, little explored. Indeed, Corbet has explicitly solicited further work in this area in print on at least two occasions (1999, 2003). Weather-related factors such as humidity and air and water temperature have been found to influence relatively minor shifts of life-history timing (e.g., Trottier 1970, 1971; Wissinger 1988). Much less often do they impact developmental regulation of odonate life-history patterns (Corbet 1999, 2003).

Developmental regulation for widespread and wide-ranging odonate species is particularly complex since the timing of a given life-history event may be highly plastic

relative to calendar dates but fixed for some environmental attribute. For example, Corbet (1999, 2003) has outlined many odonate species in which emergence may occur in August at high latitudes but in October at low latitudes but at the same air temperature for both latitudes, as well as species in which timing may be plastic for some environmental quality and fixed in date, as when emergence begins in late August across the whole species range. Moreover, several widespread odonate species are believed to engage in seasonal migrations (Russell et al. 1998). Such species are capable of nektonic, directed flight, probably spanning scales of hundreds of kilometers or more. Given that these species appear to mate and lay eggs during the migratory process (Matthews, unpublished data), high rates of gene flow over large scales should mitigate or eliminate the role of adaptation to local conditions, such as mean precipitation timing, temperature constraints, and prey abundance. Given that most mass movement events for North American migratory species have been observed during the fall, all or most such species should follow a T2 and/or T3 life-history pattern.

By far the best-studied of the alleged migrant species is *Anax junius,* a species found roughly between 15 and 50° latitude (Needham et al. 2000) with two distinct life-history trajectories (Figure 4–1). At the northern end of this range, *A. junius* exclusively pursues a T3 univoltine life-history, with adult emergence beginning in August (Walker 1958, Trottier, 1966, Catling 2003). However, a bivoltine pattern with single ponds containing overwintering T2 larvae and single-season T3 larvae is found as far north as 45° (Trottier 1971, Matthews 2004) and at least as far south as 19° latitude (Matthews, unpublished data). Other observers have documented these behaviors over a range of intermediate latitudes, including Paulson (1966), Paulson and Jenner (1971), Wissenger (1988), and May (unpublished data). An experimental study suggested that T2 *A. junius* larvae, which overwinter in a quiescent state at a mid to late instar level, require

approximately 30% more degree-days to reach maturity than T3 larvae, which develop from egg to adult between spring and late summer or early fall (Trottier 1970, 1971).

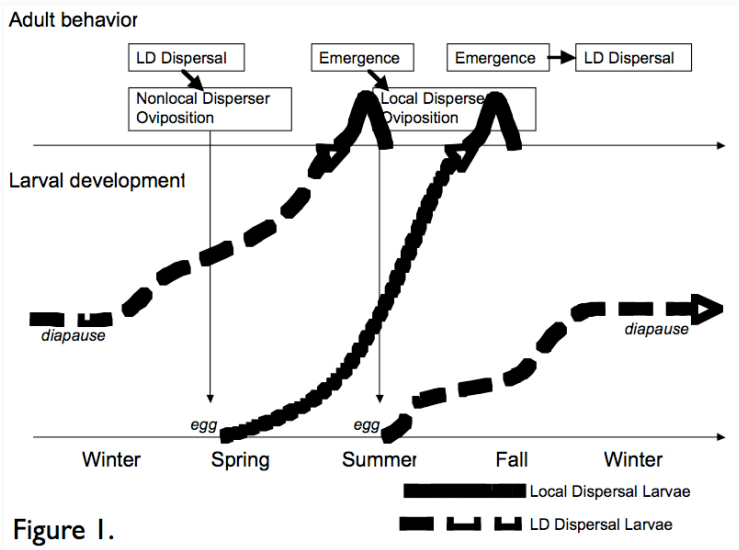


Figure 4–1. *Anax junius* life cycle, as described by Trottier (1970) and Corbet (1999).

While not directly addressing the behavior of *A. junius,* Corbet (2003) suggested that confamilials of *A. junius* between 50 and 70° latitude in North America may use photoperiod cues to regulate their life-history timing. Photoperiod — whether absolute and unchanging light-dark periods or relative changes in photoperiod — has many advantages as a cue for species found over a large latitudinal gradient, especially high latitudes where intra-annual changes in photoperiod are large, providing a powerful signal for larvae in open and ice-free water to maintain a latitude-appropriate developmental phenology. In contrast, air temperatures are a far more variable and less-reliable cue, and water temperatures are likely to serve as only a poor proxy for air temperatures (Matthews in press).

The role of photoperiod in developmental regulation has not widely been explored within the family Aeshnidae. Calvert (1929) successfully raised a single T2-trajectory *A. junius* from egg through emergence in a laboratory watchglass at room temperature. This

individual even entered a state of quiescence for some months, suggesting that while temperature influences larval growth rate it probably does not determine life-history trajectory. Photoperiod also influenced larval growth rates in *Anax imperator,* a European species congeneric with *A. junius* (Corbet 1955), though self-admittedly this work was "suggestive" rather than definitive (Corbet 2003).

Other odonate families have received more attention than the aeshnids. Among other dragonfly species (suborder Anisoptera), *Epitheca cynosura* (Say), for instance, delays or accelerates late-instar development if exposed to long or short photoperiods, respectively (Lutz 1974). Norling (1984a, 1984b) also found a photoperiod role in determining alternative emergence phenologies in *Leucorrhinia dubia* (Vander Linden). For damselflies (suborder Zygoptera), De Block and Stoks (2003, 2004) found a regulatory connection between foraging strategy, developmental phenology, and photoperiod in *Lestes viridis* (Vander Linden).

Two of these species have ranges limited to mid to high latitudes (>40°), where the difference between mid-summer and spring or fall daylengths can be many hours. Moreover, none of these species is believed to be capable of dispersal over large spatial scales comparable to *A. junius,* which can maintain distinct T2 and T3 cohorts into the tropics (i.e., <23.5° N latitude) (Matthews, unpublished data), where seasonal shifts in photoperiod are quite small relative to the northern limits of the species' range.

Additionally, landscape-level gene flow in *A. junius* would appear to oppose local adaptation to either photoperiodic cues or local weather or climatic patterns (Kingsolver et al. 2002). Although published data on continental-scale phylogeography in *A. junius* is limited, Freeland et al. (2003) found that mitochondrial haplotypes of adults and larvae showed little or no significant geographic pattern between more than a dozen sites between New Brunswick, Canada, and Hawaii, USA. Individuals that had followed a T2

versus a T3 life-history pattern also showed no significant pattern in a nested clade analysis.

Much speculation about *A. junius* has focused on adults that have followed these distinct patterns. Trottier (1971) was perhaps the first researcher to declare that the fall-emerging T3 individuals were long-distance "migrants," and that the spring-emerging T2 individuals followed a nonmigrant "resident" strategy as adults, remaining near their natal pond. These terms and views have been reinforced and taken up by other researchers (e.g., Wissinger 1988, Russell et al. 1998), though no formal tests have been made of the claims inherent in this terminology (for speculation on this topic, see Soltesz et al. 1995). Nonetheless, the association of distinct adult movement-type categories may have some relevance to understanding the basis for the presence of sympatric but distinct larval life-history patterns. If so, then the cue for larval growth trajectory would also be a cue for adult movement strategy.

In perhaps the majority of species in which migration has been studied, multiple migration strategies are evident, presenting many problems to understand the evolution and ecological maintenance of multiple strategies. Theoretical work to date has focused on the conditions that favor the evolution of multiple migration strategies, including a dependence on patchy habitat types that are only temporarily suitable for important biological functions. By contrast, more-persistent habitats are associated with decreased rates of migration (Roff 1994, Zera and Denno 1997). Migration is associated in insects in particular with evolutionary "costs" associated with fecundity, so that migration can thus be contrasted with a localized non-dispersing movement strategy. Migrant-nonmigrant patterns have indeed been observed in congenerics (Roff 1984) and separate individuals within single species (Hanski et al. 2004).

These patterns may vary slightly in systems that regularly pass through significant periods of habitat unsuitability. *Anax junius*'s primary habitat is ephemeral standing-water systems (Matthews 2004). In ephemeral wetlands, for example, aquatic insect species typically favor either an inter-patch movement period during the life-history cycle or possess traits that increase the likelihood that an individual can survive an unsuitable period in a given habitat without movement (Williams 1997). These alternate strategies may effectively serve as adaptations to unsuitable periods by moving through space (i.e., seeking another more-suitable habitat) or moving through time (i.e., waiting for a single habitat to return to a more-suitable state).

More generally, the basis for the determination of migration strategy has proven to be highly variable between insect species (Harrison 1980). A multigenerational study of the Glanville fritillary butterfly (*Melitaea cinxia* [Linnaeus]*)* found that female flight efficiency and migration propensity was inversely associated with fecundity and that these traits had a strongly heritable basis (Hanski et al. 2004). In contrast, a series of studies of gerrid water striders found that life-history patterns were primarily constrained by the degree of persistence of water bodies with a plastic component associated with distinct and alternate wing-length and flight ability forms (Vepsäläinen 1974, Jarvinen & Vepsäläinen 1975, Pfenning & Poethke 2006).

A weakness inherent to such studies is that they often simplify the basis of migration strategy to either an ecologically induced plastic migration strategy or as a strictly inherited and genetically determined phenotype. Of course, migration strategy may also vary by lineage and expression (so-called GxE expression patterns) or via maternal (or similar multi-generational) influence, both methods of determining phenotype that are often more difficult to distinguish between than simple ecological-genetic contrasts (Murren et al. 2001). In addition, migration strategy is rarely an isolated

trait. Indeed, the study of both life-history evolution and the newly defined field of niche construction (Odling-Smee et al. 2003) is essentially a study of association between suites of traits and their ecological settings. An analysis of alternate migration strategies in a single species must therefore retain a focus on the ecological setting of both the movement strategies themselves and other associated life-history traits.

With the species' high rates of gene flow and distinct movement strategies, *A. junius* is a species in which we might expect to find responses to environmental cues that are reliable over large spatial scales. If migration phenotype is determined even partially through plastic processes, then there should be a cue or similar means of phenotype inducement. Following the intuition of Corbet (1999, 2003), we agree that photoperiod should be a clear signal for determining life-history timing. Trottier showed that temperature could alter developmental rate, but he also showed that the number of degree days necessary to achieve emergence was both fixed before his experiment began (with relatively late-instar larvae) and that T2 and T3 larvae showed different degree-day thresholds. In contrast, over such a large geographic range, changing photoperiod appears more likely to provide a sufficiently reliable trigger for larval developmental regulation (and the determination of the degree-day threshold), though temperature clearly plays some kind of supporting role (Trottier 1971). We thus hypothesize that changing photoperiod is the most likely cue for larval life-history timing.

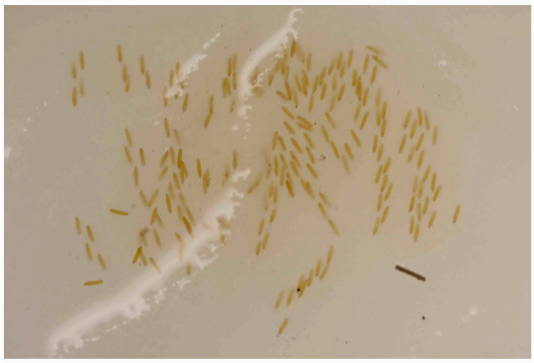

Figure 4–2. *Anax junius* eggs, laid by a gravid female in the fibers of a paper towel.

## MATERIAL AND METHODS

A split-sibling common garden experiment was designed to explore the effects of changing photoperiod on *A. junius* larval growth rates (Windig et al. 2004). Eight gravid *A. junius* females were gathered in early September 2006 at several ponds in Travis County, Texas, representing an intermediate latitude for the species' range. Immediately following their netting, females (each designated by a letter of the alphabet) were placed in 0.5-liter plastic containers with a moist paper towel in the bottom of the container, mimicking the plant fibers female *A. junius* use for oviposition (Figure 4–2). Eggs were collected in two batches. Lineages A through E entered the environmental chamber on 8 September 2006, while lineages F through H began 15 September. Each female laid between 50 and 800 fertilized eggs. A minimum of 15 eggs/female were then sampled randomly from these batches and placed within individual new 5-ounce commercial condiment cups (Figure 4–3). No data has been published on the ability of *A. junius* females to store sperm from multiple males, so eggs from a single female may be either half or full siblings.

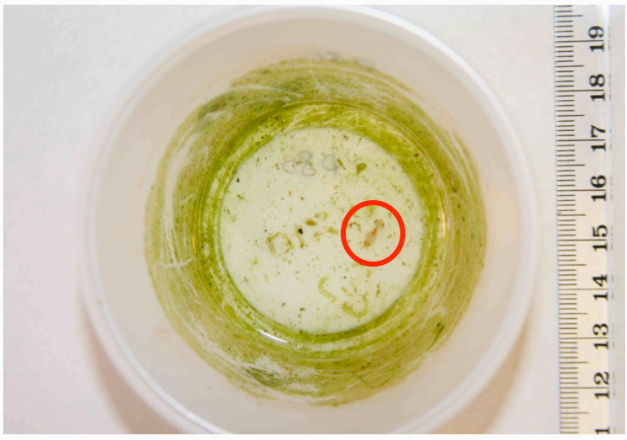


Figure 4–3. A commercial restaurant condiment cup, used to house individual *A. junius* larvae over the course of the experiment. To obtain measurements, photographs were taken of the cups with their larval denizen (here, circled), with a visual scale to enable later measurements.

At least 5 eggs/female (one egg/cup) were placed in each treatment in a three-level Percival environmental chamber, with each level corresponding to a distinct

photoperiod treatment. The treatments were increasing photoperiod, decreasing photoperiod, and constant (control) photoperiod (see Figures 4–4 through 4–6), with temperature held constant at 24°C±1.5°C (confirmed with temperature data loggers). Full-spectrum fluorescent lights were used, totaling 80 W/treatment. Initial L:D settings for each treatment, respectively, were 10:14, 12:12, and 12:12. These ratios were maintained for two days, then increased/decreased 45 minutes for the increasing/decreasing treatments, respectively, and maintained at this level 6 days. Thereafter, every 7 to 9 days the photoperiod was adjusted 30 minutes.

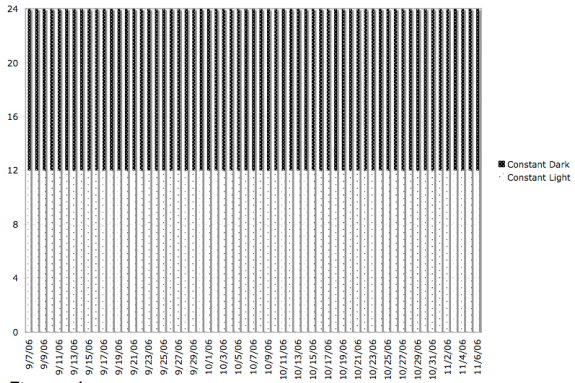


Figure 4.

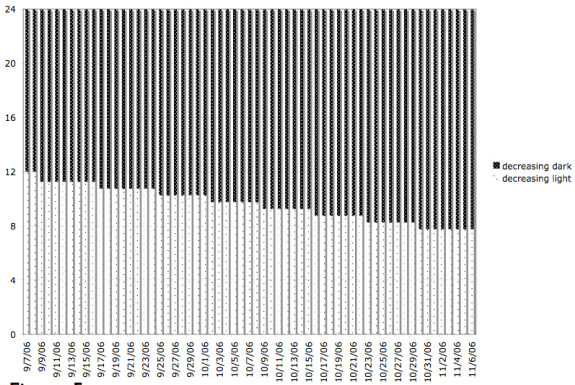


Figure 5.

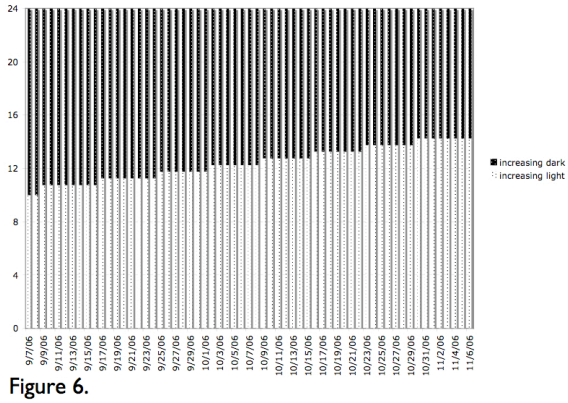


Figure 6.

Figures 4–4 through 4–6. Details of the relative light (white) and dark (black) cycles used for treatments.

Beginning 8 September 2006, cups were photographed three times/week. Until 25 September, these images were taken using an electronic scanner (during daylight treatments to reduce effects from the scanner light) and placing the cups on the face of the scanner with a ruler as a size standard. After 25 September, cups were photographed from above using a digital SLR camera to take high-resolution photos. Again, a ruler was placed within each photo for scale. Using IMAGEJ software, images were size-referenced against the ruler and then individual larval length was measured from the anterior of the head capsule to cerci/paraprocts. Final data for analysis was based on larvae that survived until the completion of the experiment (6 November 2006), tracking mean length/treatment/day.

As individual larvae hatched, food was introduced to their cups *ad libitum*. A mix of prey items including ostracods, *Daphnia* spp., copepods, and rotifers were added to each cup at least three times/week, and water levels within each cup were maintained at 3 to 4 oz using distilled water. Every two weeks, cups with dead larvae were culled.

## RESULTS

Mortality rates were high, ranging between 63 and 100% by lineage. However, a log-likelihood ratio test showed no significant survivorship differences between lineages by treatment (Table 4–1; $G = 6.879$, df = 10, p=0.74). With three blocks per treatment, there were no significant differences in survivorship within blocks when assessed 26 days before the end of the experiment (Table 4–2; constant blocks $G = 2.446$, df = 2, p=0.29; decreasing blocks $G = 0.39116$, df = 2, p=0.82; and increasing blocks $G = 4.820$, df = 2, p=0.09) and when assessed at the end of the experiment (Table 4–3; constant blocks $G = 4.251$, df = 2, p=0.12; decreasing blocks $G = 3.352$, df = 2, p=0.19; and increasing blocks $G = 1.666$, df = 2, p=0.43). On this basis, blocks within treatments will be lumped.

| Lineage | Increasing | Decreasing | Constant |
|---|---|---|---|
| A | 0.15 | 0.15 | 0.15 |
| B | 0.20 | 0.44 | 0.00 |
| D | 0.27 | 0.54 | 0.08 |
| F | 0.30 | 0.20 | 0.10 |
| G | 0.10 | 0.40 | 0.10 |
| H | 0.00 | 0.10 | 0.00 |

Table 4–1. Survivorship rates by lineage across treatment (as of 11 October, 26 days before the end of the experiment)

| Block | Treatment | Alive | Dead |
|---|---|---|---|
| 5 | Constant | 8 | 13 |
| 6 | Constant | 4 | 16 |
| 9 | Constant | 6 | 24 |
| 3 | Decreasing | 11 | 10 |
| 4 | Decreasing | 13 | 8 |
| 8 | Decreasing | 17 | 13 |
| 1 | Increasing | 4 | 18 |
| 2 | Increasing | 7 | 15 |
| 7 | Increasing | 14 | 16 |

Table 4–2. Survivorship rates by block across treatments (as of 11 October, 26 days before the end of the experiment)

| Block | Treatment | Alive | Dead |
|---|---|---|---|
| 5 | Constant | 3 | 18 |
| 6 | Constant | 0 | 20 |
| 9 | Constant | 2 | 28 |
| 3 | Decreasing | 4 | 17 |
| 4 | Decreasing | 9 | 12 |
| 8 | Decreasing | 7 | 23 |
| 1 | Increasing | 2 | 20 |
| 2 | Increasing | 5 | 17 |
| 7 | Increasing | 4 | 26 |

Table 4–3. Survivorship rates by block across treatments (as of 6 November, the last day of the experiment)

Table 4–4. Measurements and growth rates for the final set of larvae.

| ID | family | Length (cm) 10/11/06 | Length (cm) 10/16/06 | Length (cm) 10/27/06 | Length (cm) 11/6/06 | Treatment | Block | Ratio of last 11 days | Ratio of last 21 days | Ratio of last 26 days | Ratio from day 11 to day 21 | Ratio from day 21 to day 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| a80 | a | 0.357 | 0.662 | 0.690 | 0.798 | con | 5 | 1.157 | 1.205 | 2.235 | 0.959 | 1.854 |
| d4d | d | 0.408 | 0.428 | 0.441 | 0.595 | con | 5 | 1.349 | 1.390 | 1.458 | 0.971 | 1.049 |
| a89 | a | 0.422 | 0.475 | 0.571 | 0.698 | con | 6 | 1.222 | 1.469 | 1.654 | 0.832 | 1.126 |
| g8 | g | 0.293 | 0.418 | 0.544 | 0.729 | con | 9 | 1.340 | 1.744 | 2.488 | 0.768 | 1.427 |
| f22 | f | 0.368 | 0.395 | 0.536 | 0.777 | con | 9 | 1.450 | 1.967 | 2.111 | 0.737 | 1.073 |
| b5b | b | 0.469 | 0.587 | 0.698 | 0.920 | dec | 3 | 1.318 | 1.567 | 1.962 | 0.841 | 1.252 |
| a71 | a | 0.418 | 0.505 | 0.601 | 0.966 | dec | 3 | 1.607 | 1.913 | 2.311 | 0.840 | 1.208 |
| d78 | d | 0.506 | 0.500 | 0.615 | 0.898 | dec | 3 | 1.460 | 1.796 | 1.775 | 0.813 | 0.988 |
| d80 | d | 0.493 | 0.538 | 0.644 | 0.883 | dec | 3 | 1.371 | 1.641 | 1.791 | 0.835 | 1.091 |
| b57 | b | 0.483 | 0.535 | 0.743 | 1.025 | dec | 4 | 1.380 | 1.916 | 2.122 | 0.720 | 1.108 |
| d2d | d | 0.350 | 0.374 | 0.473 | 0.636 | dec | 5 | 1.345 | 1.701 | 1.817 | 0.791 | 1.069 |
| d27b | d | 0.340 | 0.338 | 0.461 | 0.595 | dec | 4 | 1.291 | 1.760 | 1.750 | 0.733 | 0.994 |
| d77 | d | 0.442 | 0.461 | 0.544 | 0.905 | dec | 4 | 1.664 | 1.963 | 2.048 | 0.847 | 1.043 |
| b54 | b | 0.589 | 0.738 | 0.835 | 0.897 | dec | 4 | 1.074 | 1.215 | 1.523 | 0.884 | 1.253 |
| a70 | a | 0.415 | 0.467 | 0.598 | 0.775 | dec | 4 | 1.296 | 1.660 | 1.867 | 0.781 | 1.125 |
| b53t | b | 0.570 | 0.600 | 0.650 | 0.740 | dec | 4 | 1.138 | 1.233 | 1.298 | 0.923 | 1.053 |
| d71 | d | 0.420 | 0.420 | 0.452 | 0.532 | dec | 4 | 1.177 | 1.267 | 1.267 | 0.929 | 1.000 |
| d72 | d | 0.463 | 0.548 | 0.606 | 1.030 | dec | 4 | 1.700 | 1.880 | 2.225 | 0.904 | 1.184 |
| g37 | g | 0.263 | 0.320 | 0.419 | 0.746 | dec | 8 | 1.780 | 2.331 | 2.837 | 0.764 | 1.217 |
| g36 | g | 0.290 | 0.398 | 0.521 | 0.851 | dec | 8 | 1.633 | 2.138 | 2.934 | 0.764 | 1.372 |
| f23 | f | 0.273 | 0.373 | 0.459 | 0.805 | dec | 8 | 1.754 | 2.158 | 2.949 | 0.813 | 1.366 |
| f36 | f | 0.257 | 0.277 | 0.416 | 0.671 | dec | 8 | 1.613 | 2.422 | 2.611 | 0.666 | 1.078 |
| g26 | g | 0.272 | 0.425 | 0.559 | 0.783 | dec | 8 | 1.401 | 1.842 | 2.879 | 0.760 | 1.563 |
| b53b | b | 0.509 | 0.559 | 0.602 | 1.075 | inc | 1 | 1.786 | 1.923 | 2.112 | 0.929 | 1.098 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| d6d | d | 0.407 | 0.468 | 0.485 | 0.703 | inc | 1 | 1.449 | 1.502 | 1.727 | 0.965 | 1.150 |
| a26b | a | 0.349 | 0.406 | 0.505 | 0.862 | inc | 2 | 1.707 | 2.123 | 2.470 | 0.804 | 1.163 |
| b51 | b | 0.421 | 0.428 | 0.692 | 0.784 | inc | 2 | 1.133 | 1.832 | 1.862 | 0.618 | 1.017 |
| a20b | a | 0.296 | 0.330 | 0.525 | 0.821 | inc | 2 | 1.564 | 2.488 | 2.774 | 0.629 | 1.115 |
| d55 | d | 0.460 | 0.433 | 0.536 | 0.844 | inc | 2 | 1.575 | 1.949 | 1.835 | 0.808 | 0.941 |
| f37 | f | 0.323 | 0.421 | 0.482 | 0.900 | inc | 7 | 1.867 | 2.138 | 2.786 | 0.873 | 1.303 |
| f9 | f | 0.301 | 0.414 | 0.458 | 0.871 | inc | 7 | 1.902 | 2.104 | 2.894 | 0.904 | 1.375 |
| f3 | f | 0.267 | 0.362 | 0.478 | 0.792 | inc | 7 | 1.657 | 2.188 | 2.966 | 0.757 | 1.356 |
| g18 | g | 0.277 | 0.360 | 0.562 | 1.001 | inc | 7 | 1.781 | 2.781 | 3.614 | 0.641 | 1.300 |
| | | | | | | | | | | | | |
| Mean: constant | | 0.370 | 0.476 | 0.556 | 0.719 | | | 1.304 | 1.555 | 1.989 | 0.853 | 1.306 |
| Mean: decreasing | | 0.406 | 0.467 | 0.572 | 0.814 | | | 1.445 | 1.800 | 2.109 | 0.812 | 1.165 |
| Mean: constant | | 0.361 | 0.418 | 0.533 | 0.865 | | | 1.642 | 2.103 | 2.504 | 0.793 | 1.182 |
| | | | | | | | | | | | | |
| Variance: constant | | 0.0026 | 0.0117 | 0.0080 | 0.0064 | | | 0.0132 | 0.0906 | 0.1796 | 0.0116 | 0.1170 |
| Variance: decreasing | | 0.0113 | 0.0132 | 0.0136 | 0.0204 | | | 0.0469 | 0.1195 | 0.2962 | 0.0052 | 0.0238 |
| Variance: increasing | | 0.0070 | 0.0041 | 0.0050 | 0.0116 | | | 0.0522 | 0.1230 | 0.3742 | 0.0166 | 0.0216 |

All measurements are based on the final surviving set of 33 larvae (10 individuals in the increasing treatment, 18 individuals in the decreasing treatment, and 5 individuals in the constant treatment). Measurements discussed here were taken on four separate days over the final 26 days of the experiment (Table 4–4, Figure 4–7). Comparisons of larval length in themselves were not significant (Figure 4–8), and whose to focus on rates of growth as a more meaningful method of evaluating change over time.

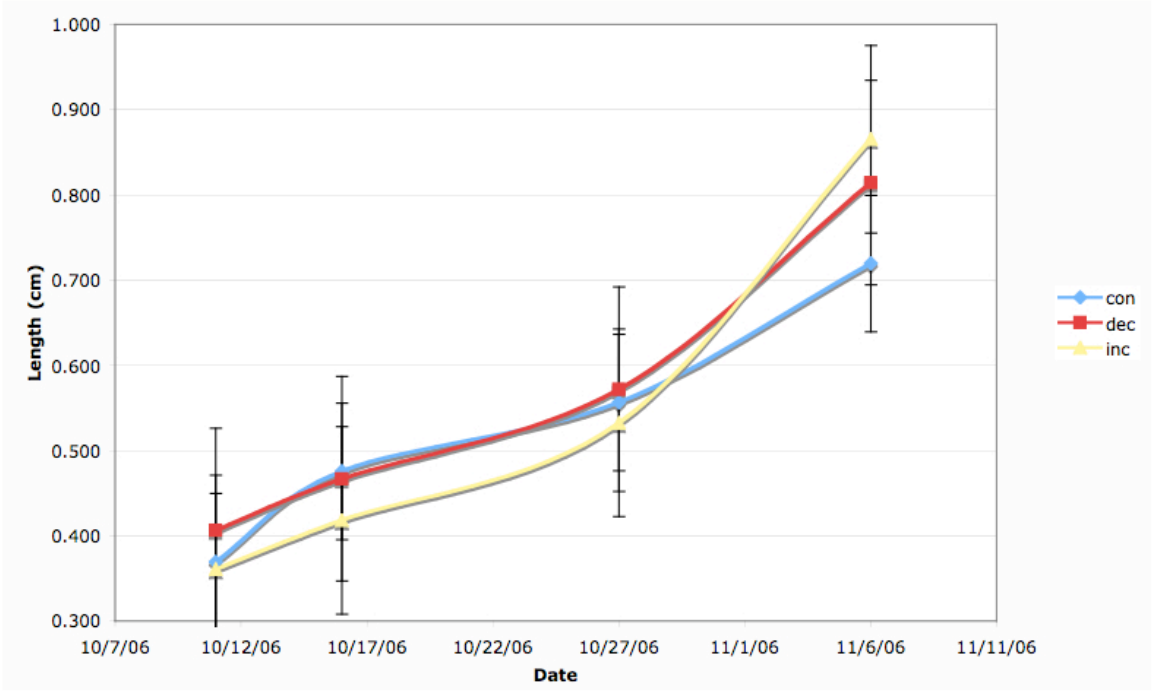


Figure 4–7. Mean larval length by treatment over the final 26 days of the experiment. Error bars show first standard deviation.

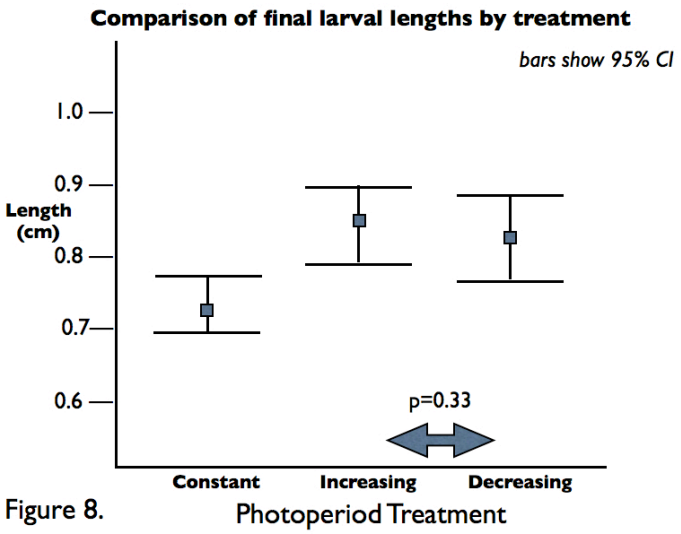


Figure 4–8. A comparison of larval lengths at the end of the experiment.

Tukey's HSD method for multiple comparisons of growth rate over the final 11 days showed a pairwise family effect for lineages B and F ($F(4,28) = 3.49$, p=0.02). Family effects were more pronounced and involved more significant pairwise family comparisons on day 21 ($F(4,26) = 15.58$, $p<0.001$; Figures 4–9 through 4–11).

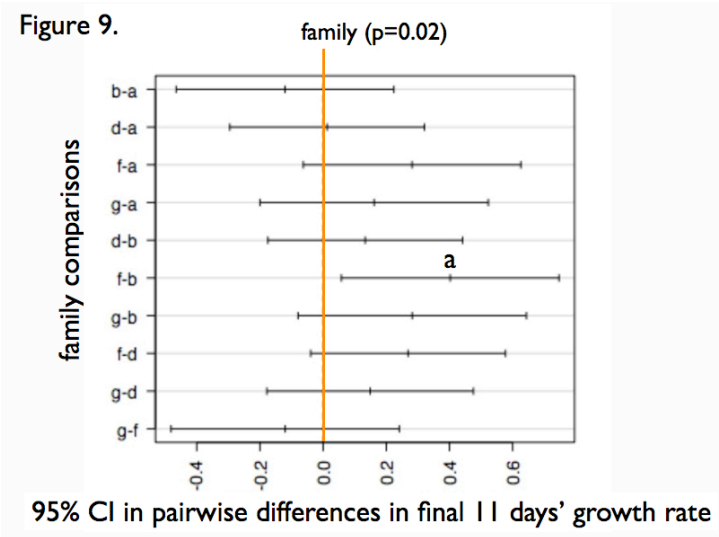


Figure 4–9. The effect of family on growth rate over the final 11 days of the experiment.

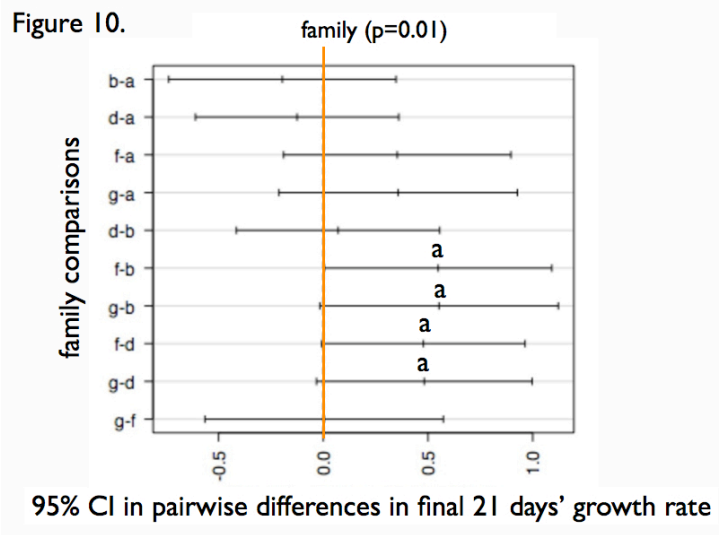


Figure 4–10. The effect of family on the growth rate over the final 21 days of the experiment.

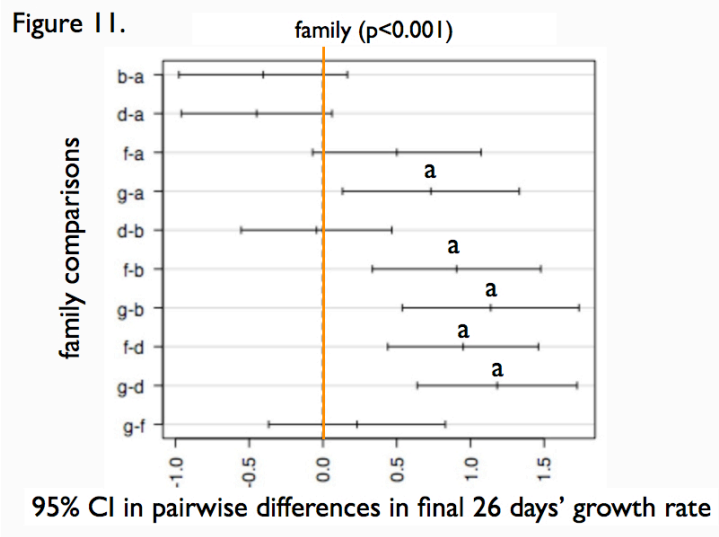


Figure 4–11. The effect of family on the growth rate over the final 26 days of the experiment.

Growth rates were also compared by treatment. Overall differences between treatments were only significant in the final ten days (Figure 4–12; $F(2,30) = 5.005$, p=0.01). However, the increasing photoperiod group was significantly faster than the decreasing photoperiod group over two periods: the final 10 days ($F(2,33) = 5.145$, p=0.03), and the final 21 days ($F(2,33) = 4.878$, p=0.04) (Figures 4–13 and 4–14). The increasing group also grew significantly faster than the constant-photoperiod group during both periods (last 10 days: $F(1,13) = 9.501$, p=0.009; last 21 days: $F(1,13) =$

8.845, p=0.01), but while the decreasing group was consistently larger than the constant group, these differences were not significant (last 10 days: $F(1,21) = 1.918$, p=0.18; last 21 days: $F(1,21) = 2.064$, p=0.17). Likewise, no significant differences existed between the three groups over the final 26 days of the experiment (Figure 4–14; $F(2,30) = 2.123$, p=0.14), nor were there significant differences between groups for the periods between day 21 and day 11 ($F(2,30) = 0.6495$, p=0.53) or between day 26 and day 21 ($F(2,30) = 1.115$, p=0.34) (Figures 4–15 and 4–16).

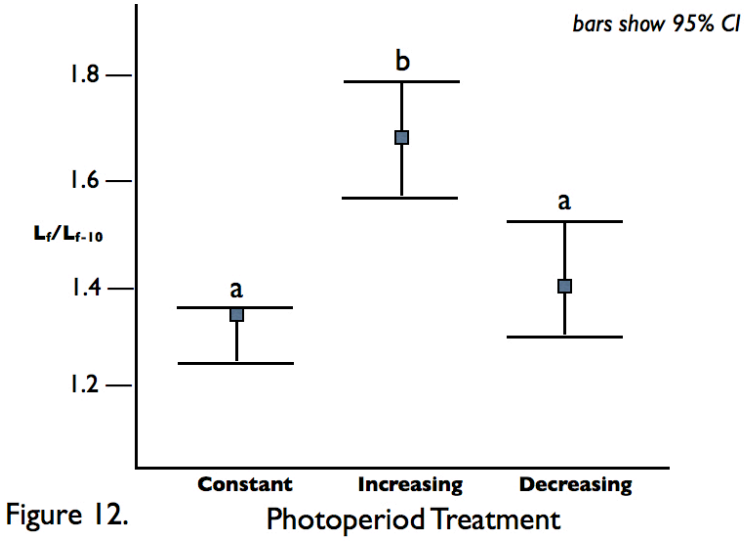


Figure 12.

Figure 4–12. Comparison of the last 11 days of growth by treatment.

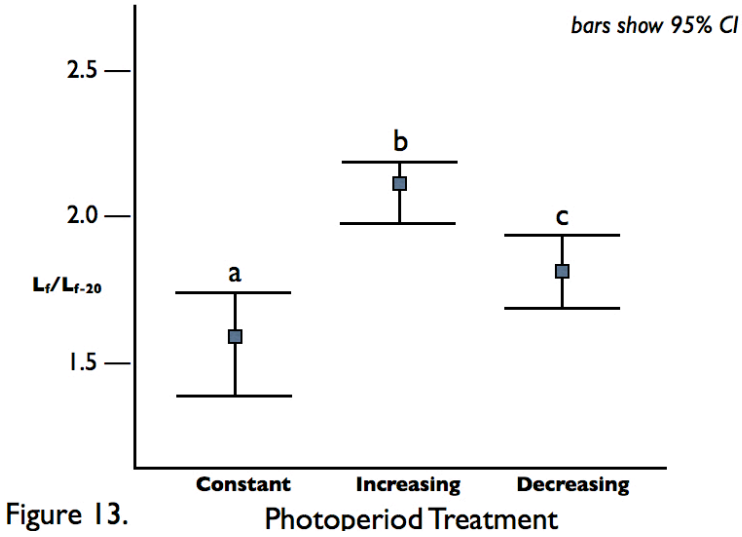


Figure 13.

Figure 4–13. Comparison of the last 21 days of growth by treatment.

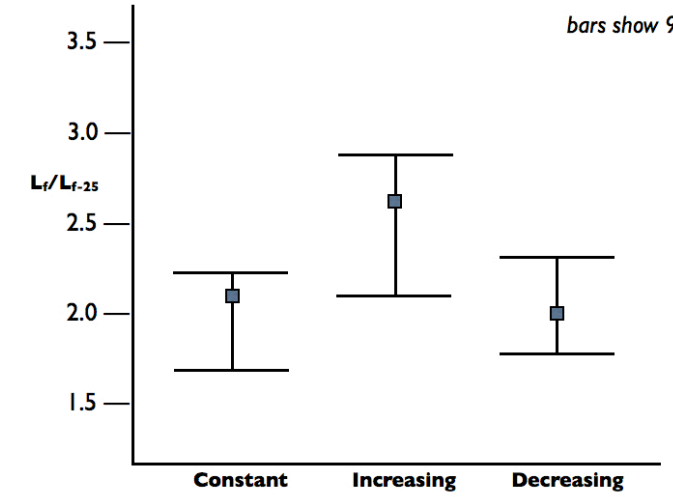


Figure 14.

Figure 4–14. Comparison of the last 26 days of growth by treatment.

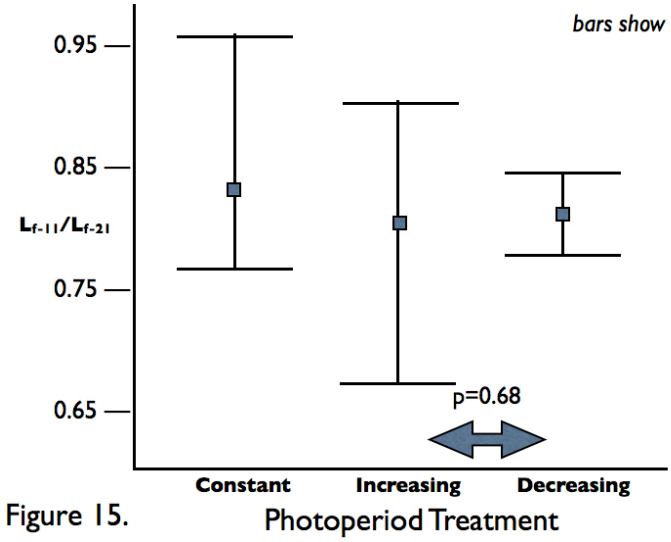


Figure 15.

Figure 4–15. Comparison of growth from f-21 to f-11 by treatment.

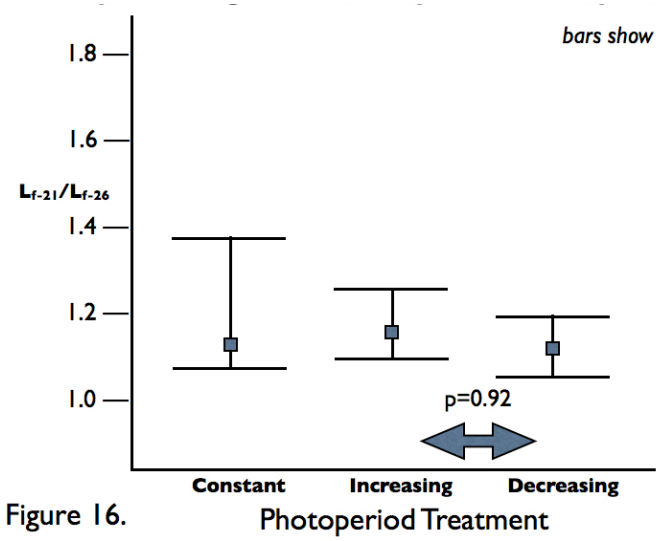


Figure 16.

Figure 4–16. Comparison of growth from day f-26 to f-21 by treatment.

## DISCUSSION

Increasing photoperiod triggered a significantly faster larval growth rate than the decreasing and constant photoperiod treatments during the last three weeks of the experiment. These difference show that larvae oviposited during the spring — between the vernal equinox and the summer solstice in the northern hemisphere — develop during through their middle instars at a faster rate than larvae whose eggs are laid after the summer solstice. Photoperiod plays a major role in helping *A. junius* larvae select between alternative developmental pathways, which in turn determine adult movement strategy.

Given the uniform distribution of haplotypes between T2 and T3 individuals reported by Freeland et al. (2003) and the presumption of adult reproductive movement over hundreds of kilometers (Russell et al. 1998), local adaptation is unlikely to play a significant role in *A. junius* developmental regulation in favor of some external signal for phenotype. Corbet's contention (1999, 2003) that absolute or changing photoperiod would be a likely signal at high latitudes for developmental regulation also appears to apply at mid and low latitudes — at least in *A. junius*. Moreover, we did not begin the

experiment using the extreme photoperiods typical of high latitudes, which suggests that *A. junius* could be capable of receiving "weak" signals successfully.

The lack of significant differentiation between constant and decreasing treatments provides an unclear result in this regard. The constant treatment did not represent an intermediate rate of growth between the increasing and decreasing treatments. Instead, the constant treatment consistently lagged behind the decreasing in growth rate. Since the constant treatment most approximated near-equatorial latitudes and equinoctial seasons, a different set of light conditions might reveal a distinct low-latitude development cycle. However, given the current data we cannot distinguish between this hypothesis and the inability of larvae to detect any signal at all. A repetition of this design using constant but unequal light-dark periods might resolve between these issues.

Temperature, of course, is the "other" important north-south gradient observable across the full range of *A. junius*. Temperature clearly alters rate of growth, but Trottier's (1970, 1971) estimate of the degree-days necessary for T2 and T3 larvae to reach an emergence threshold proved fixed. In light of our results, however, changing photoperiod determines phenotype (and the ultimate number of degree days necessary for emergence), and ambient temperature determines the relative rate that this number of degree days is achieved. The interaction between photoperiod and temperature thus appears to determine both the cross-latitudinal gradient for emergence phenology and site-specific intra-annual as well as intra-latitude variation in emergence timing. Temperature alone is unable to explain the relative fixity of emergence dates at single sites (e.g., Trottier 1971, Wissinger 1988). Moreover, if temperature alone were a cue then it might dislodge the relative phenology of T2 and T3 larvae, a phenomenon that has never been observed over several decades of research.

On the other hand, temperature may play a powerful role to reinitiate growth following the end of the period of arrested development seen in the overwintering T2 larvae, signaling an end to winter. Although this pattern might explain latitudinal differences in the timing of spring emergence in T2 individuals, this hypothesis must be tested experimentally. Calvert's watchglass specimen (1929), for instance, presumably received only weak temperature cues in a laboratory setting before leaving its quiescent state.

An interesting implication of differences in total degree-days necessary for emergence for larvae with different life-history trajectories is that an array of physiological resources are allocated differently for each larval and adult developmental pathway. In many insect species, faster development often corresponds to smaller size or other tradeoffs, such as fecundity (Zera and Cisper 2001, Zera and Harshman 2001, Hanski et al. 2004) or resistance to starvation (Gotthard et al. 1994). A thorough study of a variety of metrics between T2 and T3 pathways would be a productive exploration.

While development rate in *A. junius* clearly has a strong plastic component, the scale of this experiment precluded the exploration of GxE effects that would document inherited differences in plasticity response. There are some tantalizing suggestions, however, in the strength of family effects and in how these effects evolved over the last three weeks of the experiment. The effect of family is significant ($p=0.02$) for the final 11 days, but the strength of significance increases when looking over the last 21 days ($p=0.01$) and the last 26 days ($p<0.001$), while the number of families showing significant pairwise differences in growth rate declines from five at day 26 to four at day 21 to one at day 11. Thus, the influence of family became less pronounced as the experiment proceeded, suggesting that inter-family differences become less importance as larval development proceeds and resulting in more-uniform — perhaps more

cannelized? — life-history paths with time. The import of these effects is especially significant since we cannot assume that larvae sharing a mother are more than half-sibs. Odonates are well known among behavioral ecologists for the ability within many species for females to store sperm from multiple fathers and for males to attempt to remove the sperm from previous matings (Waage 1979) — most famously in the suborder Zygoptera but probably also in many Anisoptera (which includes *A. junius*). Not least as an issue, family effects are notoriously difficult to quantify even though in most cases they are found when sought out (Windig et al. 2004). Unless family effects are strong, power for family studies is often low. Indeed, the power to look for GxE effects in this sample is clearly too low.

The effect of photoperiod was only significant when examining larval growth rates, not absolute size of larvae. Why should larval length not also reflect the effects of photoperiod? If the experiment had run longer, size would probably become a significant factor in distinguishing treatments, particularly if (as Calvert [1929] found in his watchglass specimen) the T2 individuals entered a non-temperature dependent quiescence or diapause and ceased growing for some period while the T3 larvae continued their growth unabated. The experiment was halted, however, before development paused in the T2 short-photoperiod treatment larvae.

The high mortality rates among the treatments and blocks was the basis for the decision to end the experiment. Clearly the most powerful evidence that photoperiod acts as a cue for larval growth rates would come from direct measures of larval growth through the final instar. Based on the mortality rates seen in this experiment, a final sample size of 36 individuals after three months in a growth chamber would require an initial starting group of at least 300 to 400 larvae rather than the 240 used here. Improvements in rearing technique would also be a critical component.

There are several other questions that would also be useful directions for further work. For instance, we assumed that changing photoperiod would provide the strongest signal for developmental regulation, but a fixed photoperiod might be sufficient, especially if larvae have a critical period during which their pathway is set. Indeed, the use of fixed long, short, and constant photoperiods for some period early in development followed by exposure to only constant photoperiod would be a means of isolating potential critical periods. Likewise, a comparison of hatch date may serve to isolate differences between treatments and suggest plasticity at a very early stage. By extension, the experimental work on photoperiod treatment with *E. cynosura* was based on late-instar larvae, as was much of the experimental work on temperature by Trottier (1970, 1971) with *A. junius* larvae. Responses to photoperiod treatment at this stage would suggest that no critical period exists for *A. junius* and that larvae can shift their developmental track mid-stream. If true, the larvae are no doubt grateful that this does not often happen in the wild.

The presumption by Freeland et al. (2003) that little or no phylogeographic structure exists for *A. junius* may simply be a reflection of using a single coarse mitochondrial marker. Thus, in addition to a comparison of GxE effects, a comparison using eggs taken from adults captured at high- and low-latitude sites would be informative in looking at latitudexGxE effects (e.g., Hill and Gatehouse 1993).

Regardless of the direction future experiments take, the plastic response to changing photoperiod seen in *A. junius* larval growth rates represents a novel but potentially widespread set of solutions to balance continental-scale movement with latitudinal variation in habitat suitability and resource availability.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**

Bégin, M., D.A. Roff, and V. Debat. 2004. The effect of temperature and wing morphology on quantitative genetic variation in the cricket *Gryllus firmus*, with an appendix examining the statistical properties of the Jackknife-MANOVA method of matrix comparison. *Journal of Evolutionary Biology* 17, 1255–1267.

De Block, M., and R. Stoks. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology* 16, 986–995.

De Block, M., and R. Stoks. 2004. Life history responses depend on timing of cannibalism in a damselfly. *Freshwater Biology* 49, 775–786.

De Block, M., and R. Stoks. 2005. Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. *Oikos* 108, 485–494.

Boivin, T., J-C Bouvier, D. Beslay, and B. Suphanor. 2004. Variability in diapause propensity within populations of a temperate insect species: interactions between insecticide resistance genes and photoperiodism. *Biological Journal of the Linnean Society* 83, 341–351.

Calvert, P.P. 1929. Different rates of growth among animals with special reference to the Odonata. *Proc. Am Ento Soc* 68(3): 227–274.

Catling, P.M. 2003. *Anax junius* overwintering in eastern Ontario. Pp. 9-10 in P.M. Catling, C. Jones, and P. Pratt, *eds., Ontario Odonata* vol. 4, Toronto Entomologist's Association, Toronto, Canada.

Corbet, P.S. 1955. The immature stages of the emperor dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *Entomological Gazette* 6, 189–204.

Corbet, P.S. 1957. The life-history of the emperor dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *Journal of Animal Ecology* 26, 1–69.

Corbet, P.S. 1960. Seasonal regulation. Pp. 138–48. In P.S. Corbet, C. Longfield, and N.W. Moore, *Dragonflies*. London: Collins.

Corbet, P.S. 1999. *Dragonflies: behavior and ecology of Odonata.* Ithaca: Cornell University Press.

Corbet, P.S. 2003. A positive correlation between photoperiod and development rate in summer species of Odonata could help to make emergence date appropriate to latitude: a testable hypothesis. *Journal of the Entomological Society of British Columbia* 100, 3–17.

Corbet, P.S., and S.A. Corbet. 1958. Emergence of a summer species of dragonfly. *Nature* 182, 194.

Freeland, J.R., M. May, R. Lodge, and K.F. Conrad. 2003. Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner (*Anax junius*). *Ecological Entomology* 28(4):413–421.

Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life-history costs and consequences in the speckled wood butterfly (*Parage aegeria)*. *Oecologia* 99: 281–289.

Hanski, I., C. Erälahti, M. Kankare, O. Ovaskainen, and H. Sirén. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7: 958–66.

Harrison, R.G. 1980. Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics* 11:95–118.

Hill, J.K., and A.G. Gatehouse. 1993. Phenotypic plasticity and geographical variation in the prereproductive period of *Autographa gamma* and its implications for migration in this species. *Ecological Entomology* 18(1): 39–46.

Jarvinen, O., and K. Vepsäläinen. 1975. Wing dimorphism as an adaptive strategy in water-striders (*Gerris)*. *Hereditas* 84(1): 61–68.

Kingsolver, J.G., D.W. Pfennig, and M.R. Servedio. 2002. Migration, local adaptation, and the evolution of plasticity. *TREE* 17(12): 540–41.

Lank, D.B., R.W. Butler, J. Ireland, and R.C. Ydenburg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103(2): 303-319.

Lutz, P.E. 1974. Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura* (Odonata: Libellulidae). *Ecology* 55, 370–377.

Matthews, J.H. In press. "Anthropogenic climate change impacts on aquatic macroinvertebrates: a thermal mass perspective." In *Odonate conservation: climate change impacts and monitoring strategies,* Jürgen Ott, ed. Sofia, Bulgaria: Pensoft Publishers.

Matthews, J.H. 2004. Report on *Anax junius* emergence in Caledon, Ontario, in 2003. *Ontario Odonata,* vol. 5.

Murren, C.J., R. Julliard, C.D. Schlichting, and J. Clobert. 2001. Dispersal, individual phenotype, and phenotypic plasticity. In *Dispersal*, edited by J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols. New York: Oxford University Press.

Needham, J.G., M. J. Westfall, and M.L. May. 2000. *Dragonflies of North America*. Gainesville, FL: Scientific Publishers.

Norling, U. 1984a. Life history patterns in the northern expansion of dragonflies. *Advances in Odonatology* 2, 127–156.

Norling, U. 1984b. Photoperiodic control of larval development in *Leucorrhinia dubia* (Vander Linden): a comparison between populations from northern and southern Sweden (Anisoptera: Libellulidae). *Odonatologica* 13, 529–550.

Odling-Smee, F.J., K.N. Laland, M.W. Feldman, and L.J. Schaaf. 2003. *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.

Paulson, D.R. 1966. Dragonflies (Odonata: Anisoptera) of South Florida. Ph.D. Dissertation, University of Miami, 603 pp.

Paulson, D.R., and C.E. Jenner. 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 52: 96-107.

Pfenning, B., and H.J. Poethke. 2006. Variability in the life history of the water strider *Gerris lacustris* (Heteroptera: Gerridae) across small spatial scales. *Ecological Entomology* 31(2), 123–130.

Roff, D.A. 1984. The cost of being able to fly: a study of wing polymorphism in two species of crickets. *Oecologia* 63(1), 30–37.

Roff, D.A. 1994. Habitat persistence the evolution of wing dimorphism in insects. *American Naturalist* 144(5), 772–798.

Russell, R.W., M.L. May, K.L. Soltesz, and J.W. Fitzpatrick. 1998. Massive swarm migrations of dragonflies (Odonata) in Eastern North America. *American Midland Naturalist* 140:325-342.

Soltesz, K., B. Barber, and G. Carpenter. 1995. A spring dragonfly migration in the Northeast. *Argia* 7(3):10-14.

Trottier, R. 1966. The emergence and sex ratio of *Anax junius* Drury (Odonata: Aeshnidae) in Canada. *Canadian Entomologist* 98, 794–798.

Trottier, R. 1970. Effect of temperature and humidity on the emergence and ecdysis of *Anax junius* (Odonata: Aeshnidae). Doctoral dissertation, University of Toronto, Toronto, Ontario, Canada.

Trottier, R. 1971. Effect of temperature on the life-cycle of *Anax junius* (Odonata: Aeshnidae) in Canada. *Canadian Entomologist* 103: 1671-1683.

Vepsäläinen, K. 1974. The Life Cycles and Wing Lengths of Finnish Gerris Fabr. Species (Heteroptera, Gerridae). Helsinki, Finland: Societas pro Fauna et Flora Fennica.

Waage, J.K. 1979. Dual function of the damselfly penis: sperm removal and transfer. *Science* 203:916-918.

Walker, E.M. 1958. *The Odonata of Canada and Alaska*. Vol. 2. Toronto: University of Toronto Press.

Williams, D.D. 1997. Temporary ponds and their invertebrate communities. *Aquatic Conservation* 7, 105–117.

Windig, J.J., C.G.F. de Kovel, D. de Jong. 2004. Genetics and mechanics of plasticity. Pp. 31–49, in T.J. DeWitt and S.M. Scheiner (eds), *Phenotypic Plasticity: Functional and Conceptual Approaches*. New York: Oxford University Press.

Wissinger, S.A. 1988. Life history and size structure of larval dragonfly populations. *Journal of the North American Benthic Society* 7, 13-28.

Zera, A.J., and R.F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* 42, 207–230.

Zera, A. J., and G. L. Cisper. 2001. Genetic and diurnal variation in the juvenile hormone titer in a wing-polymorphic cricket: Implications for the evolution of life histories and dispersal. *Physiol. Biochem. Zool.* 74:293-306.

Zera, A.J., and L.G. Harshman. 2001. The physiology of life-history trade-offs in animals. *Annu. Rev. Ecol. Syst.* 32:95–126.

# Chapter 5

## Species Richness and Abundance Estimates: What and How Often Should We Count?[1]


**ABSTRACT**

While a variety of methods of for estimating bird abundance and diversity have been used for many decades by North American resource managers, there is little consensus comparing the effectiveness of different methods in the same locality, for the same community, and over the same study period. We hypothesized that distance sampling would prove to be a more accurate and powerful basis for describing avian communities than a breeding-bird census (BBC) style survey. We tested these approaches at two National Guard properties in Central Texas over a 14-month period. Distance sampling provides a more accurate measure of community diversity and relative abundance given sufficient time during the study period, while a BBC approach is more effective if field surveys are limited in number and frequency. A BBC approach may also prove more effective at capturing rare, low-abundance species, but is much less effective at distinguishing between the relative abundance of species that are more locally common.


[1] John C. Abbott was a significant collaborator on this chapter.

## INTRODUCTION

Although scientific data on North American bird abundance and diversity dates back to the nineteenth century, much debates still exists about how to estimate avian diversity and describe local avifauna accurately. Indeed, the current diversity crisis is in part also a crisis in conservation methodology. Diversity is one of the most basic means of characterizing the biota of a particular locale, yet it is a difficult parameter to estimate, measure, and even define. For the purposes of this project, we will limit diversity as a first-order concept to species richness and as a second-order concept to abundance of one species *vis a vis* other species. Both measures are critical to habitat- and community-based approaches to resource management, but methods for estimating either have remained largely idiosyncratic and unsubstantiated as diagnostic tools. Only within the past few decades have statistically sound and robust measures begun to be developed, though the soundness of these methods has rarely been tested beyond theoretical and modeling studies that may not reflect the practical realities of fieldwork. Thus, measures of diversity may not be accurate or useful methods as a basis for resource management strategies on the ground. The soundness of these measures is even more critical given that most diversity studies are conducted with limited funding and constrained study periods. Given a shortage of time and money, what are the best methods of estimating how many taxa are present in an area and their relative abundances?

This study will focus on methods of estimating avian diversity. Birds and primates are arguably the most-studied vertebrate orders worldwide, though birds are much more widespread and generally more abundant than primates. Worldwide, bird diversity is often used as an indexes of ecosystem health and integrity, and much attention has been paid to detecting and identifying avian species. Moreover, avian

natural history is better understood (and has been understood longer) than for almost any other orders.

This study will also focus on two quite different methods of estimating diversity: presence methods and distance sampling. Presence methods are arguably the oldest means of determining species richness, but more recent efforts have attempted to link inferences about presence-absence to delimiting species ranges and, most recently, relative abundances of species (refs). Many of the long-running diversity datasets consist of presence-absence information, such as the Audubon Society Christmas bird counts, which date back to the nineteenth century in several localities. Non-traditional scientific datasets such as oral histories collected from indigenous cultures can also be interpreted as presence data and have served as meaningful long-term records for climate change studies (e.g., Sagarin & Michelli 2001). Breeding bird surveys have effectively become the standard for avian diversity studies in recent decades, yet these are at best only a more formal and rigorous form of presence methods (Bibby et al. 1998).

Distance sampling was developed much more recently based on information-theoretic approaches to richness and abundance estimation (Buckland et al. 2001). Distance sampling assumes that the ability to detect and identify an individual decreases with distance from the observer and that this detectibility can be formally estimated as a linear function. A set of identifications or registrations (when collected with data about the distance of the individual from the observer) can then be evaluated against the detectiblity function using a model-selection criterion (e.g., AIC). If the registrations match the function within some level of goodness of fit, then they can be used as a basis to estimate abundance over the study area.

While academic research has begun to shift more towards distance sampling, much NGO and GO conservation research remains based in more traditional presence

methods. The limited literature comparing the methods suggests that presence methods are better estimates of diversity when the period of research is limited to a handful of trips and for relative abundance measures, and that distance sampling provides a better estimate of absolute abundance and richness (Bibby 2001). Rare species are often of critical conservation importance, yet these are also the species that typically present the most challenges to statistical inference because of their rarity. Less data means less-powerful analysis, and no studies to date have compared the ability of presence and distance sampling methods to detect and assess rare species abundance. This research will focus on comparing and contrasting the results of distance sampling and presence methods on the bird species found at two National Guard training camps in east-central Texas, which will each be discussed in turn. These camps are located approximately 60 km apart but given their ecological and land-use contexts contain significantly different avian communities. A final section will attempt to integrate the findings from each site.

This research will also explore how richness and abundance vary through space and time across each camp and the conservation implications arising from both detection methods to maintain and improve avian community health.

## CAMP SWIFT SURVEYS

### Site Description

Camp Swift is located southeast of Elgin, Texas, and north of Bastrop, Texas (see inset, Figure 5–1). Most of the land surrounding the base is currently in mixed agricultural use. The current rural character of this region, however, is in stark contrast to the 1940s. Founded in 1942 with over 52,000 acres (21,000 hectares), Camp Swift developed into a massive training area for infantry troops bound for the battlefields of the second world war and as a prisoner of war camp for north African campaign Axis soldiers. At its

height, Camp Swift held more than 90,000 U.S. troops simultaneously. Shortly after the 1941 Pearl Harbor, Hawaii, attack by the Japanese, federal money was allocated to acquire the land for Camp Swift from local landowners (who had mostly been farmers), and a large land clearing and building construction phase began. After the end of hostilities in 1945, Camp Swift was subdivided and substantially repurposed, with some areas becoming a state prison, a cancer research facility, and a state park, as well as some land returning to private ownership. For the latter properties, the land returned to uses it had deviated from during the war and its immediate aftermath.

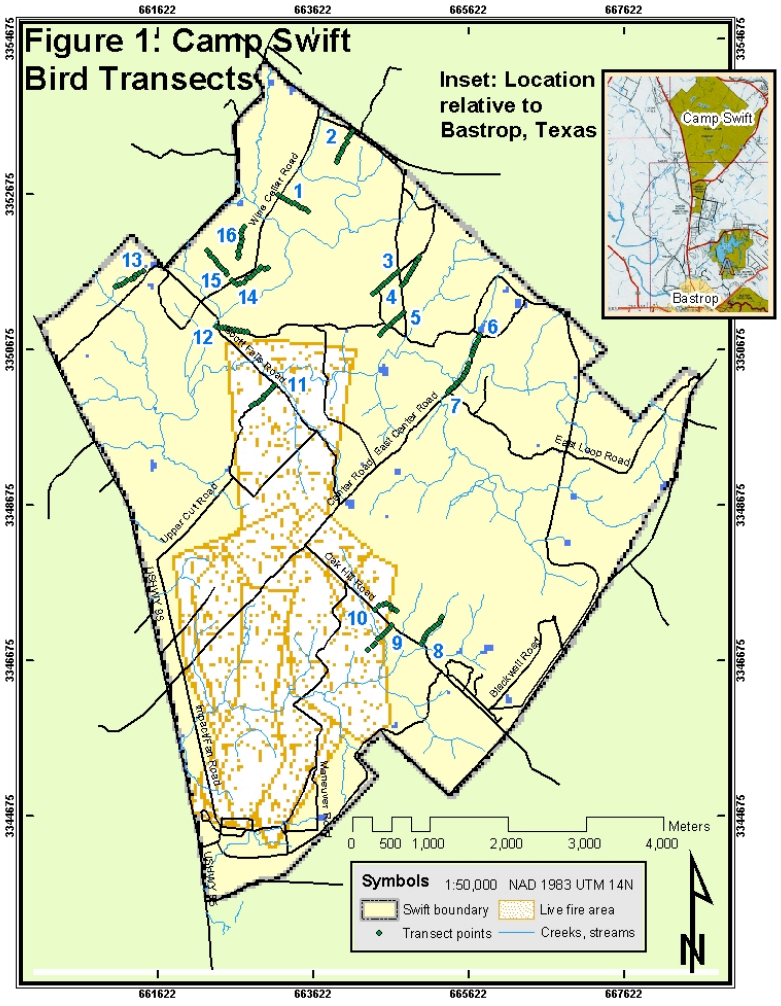



Figure 5–1. Camp Swift and its physiographic context.

The area now known as Camp Swift is a portion of the original base with 11,700 acres (4700 hectares), about 23 percent of the original extent of the camp at its height in 1942. The rural character of the region around Camp Swift is in a period of

rapid transition, particularly along US 290 and TX 71, to the north and south of Camp Swift, respectively. Both highways are serving as major arteries for residential and light industrial development for the greater Austin region. In a sense, Elgin and Bastrop appear to be shifting from roles as centers of rural commerce to suburban or exurban bedroom communities for Austin. During the period of our surveys, for instance, we noted at least eight new major (i.e., tens of hectares) housing subdivisions starting between Manor and Elgin on US 290, and signs went up announcing a new planned community immediately to the west of Camp Swift in the fall of 2004. Ecologically, these trends suggest that Camp Swift will constitute an increasingly isolated island of habitat, particularly of forested and oldfield habitats. This transformation may occur more rapidly if US 290 is expanded just north of Camp Swift or if Bastrop county lignite mining moves closer to the base.

Within the boundaries of Camp Swift, the history of land use also appears complex. Although we could not find a detailed history of those changes, some facts can be inferred. Photos of Camp Swift from its period of peak intensity wartime usage show a landscape clear of trees and shrubs and even, in some cases, groundcover vegetation such as grasses. Scattered large oaks appear in the background of some photos. The transformation of agricultural fields into training facilities appears to have taken much of the biomass of the land (and probably much of the topsoil) along with it.

Camp Swift today, however, is remarkably different. There are scattered old oaks and pines, but much of the remaining land alternates between oak–eastern red cedar (*Quercus* spp. and *Juniperus virginiana*, respectively) woodland, oak savannah, patches of pine woodland (*Pinus* spp., mostly *P. taeda*), and large stretches of meadowlike open oldfields. Most forested areas date back several decades, probably back to the 1950s, with some much older trees interspersed.

These inferences also suggests that the land was essentially recolonized from isolated habitat patches remaining from the second world war and from adjoining less-disturbed properties (though this process was no doubt slowed by the powerful drought affecting central Texas during the 1950s). Thus, we believe that the ecological history of Camp Swift is probably divided into several distinct periods: pre-European settlement, small farm agricultural use (late nineteenth century through 1941), a brief "urbanization-militarization" (1942–1950) period, and a post-urban agricultural-use period (1950 to the present). If regional trends hold true for agriculture in the Camp Swift area, then most farmers have moved from field crops to ranching since the 1960s.

Geologically, Camp Swift rests on old Tertiary sandstone, in contrast to areas immediately to the west, which are still in the great line of Cretaceous limestone bedrock extending across the state from southwest to northeast. To the east, Tertiary surface rocks grow increasingly younger towards the Gulf plain. Because of Camp Swift's close proximity to Cretaceous surface rocks, however, there are significant changes in soil hydrology and vegetation between Camp Swift and even nearby cities to the west such as Manor, while local vegetation and much of the fauna are more similar to the biota of eastern and north-central Texas. Details of the flora are presented in a separate survey (see report by Damude et al. 2005). Beneath much of Bastrop County lies a rich bed of lignite coal, which is being stripmined in several portions of the county. This formation extends under Camp Swift.

The oldfields are, to the best of our knowledge, maintained via a burn regime. Water sources are primarily small permanent and ephemeral streams, with a number of ponds and wetlands. All water bodies' habitats fluctuated widely in water volume during the survey period, often across several orders of magnitude. Relative to winter and late

spring, very little standing water was available during the late summer and early fall, when most ephemeral ponds and streams became dry for a number of months.

Current military activity is most intensive in the southern, especially southwestern, portions of Camp Swift; this land is also clearly the most disturbed and urbanized. The active firing range extends from this region due north (Figure 5–1). This region may also contain some of the most active sources of pollution as well, derived from a slaughterhouse/rendering plant just over the southern border of Camp Swift, where stormwater runoff comes from the adjoining portion of the military property. Other common sources of habitat degradation from military usage are soil erosion from the movement of heavy vehicles along sandy roads and point-source pollution from old weapons. We have no quantified data on the latter, but we did note that in many areas casings from small arms littered the ground, even in some wetland areas. Along the western portions of the border, habitat type merges fairly continuously with neighboring properties, but to the south, east, and north, most of the habitat on Camp Swift changes suddenly at the property line, usually into cattle pasture with little or no woody vegetation.

## METHODS

### Comparison of Survey Techniques

Broadly speaking, the standard resource management techniques for sampling avian richness and abundance are (1) mistnetting, (2) timed counts, and (3) presence-absence records. Mistnetting requires highly skilled workers in order to reduce sampling mortality, particularly when also leg-banding, and is time consuming to set up for each visit (Bibby et al. 1998). Net placement must accurately represent habitat diversity to reduce bias in estimates of abundance and richness. Mistnetting can reveal more silent or

visually cryptic species, especially those that make use of resources near ground levels. But mistnetting is a poor estimator of species that use upper canopy levels and perhaps even for nonpasserines generally. Sparrows, for instance, would be well represented by mistnetting, though hawks, woodpeckers, and flycatchers are likely to be weakly sampled in relative terms (Bibby et al. 1998).

Time point-counts vary greatly in complexity. Breeding bird censuses (or breeding bird surveys, also known as BBS) are one of the oldest systematic methods of estimating avian richness and abundance and have been widely used for decades in the United States and Europe. The method is simple: visit a designated point and note the number and species of all birds seen for a defined period, typically three minutes, which is often broken up into two periods of recording species and one "resting" period. Some refinements include estimates of distance from the observation point or alternate categories of distance, such as greater or less than 50 meters. Traditionally these surveys are conducted in the spring when many species are establishing and defending territories, though the technique is often used at other times of the year or as a component of long-term monitoring. Territory mapping is a related technique most appropriate for measuring the spatial extent of habitat used by breeding pairs of particular species (Bibby et al. 1998).

A more sophisticated timed point-count method is based on distance sampling, which assumes that the ability to accurately detect and identify species varies in a predictable way with distance from the observer. The method requires accurate estimates of distance from a point or transect, and software such as Distance (Thomas et al. 2004) to calculate these distances and fit detection curves of abundance to the displacement from the transect to the organism of interest, thereby generating abundance or density landscapes. Distance sampling is the only method we are aware of that purports to

estimate absolute rather than relative abundance, but few published studies employing distance sampling are concerned with more than a handful of species (e.g., Palka 1996, Jimenez et al. 2003). Further, many bird researchers who use distance sampling combine timed point counts arranged along a transect or point-transect counts rather than isolated point-counts (Bibby et al. 1998, Buckland et al. 2001, Buckland in press). Negative qualities about the method include the need to accurately measure distance and angle from the point or transect and the much more extensive preparation and training costs associated with the method relative to timed point-counts. Assumptions regarding the evenness of habitat and bird densities, for instance, are important considerations in study design, though in practical terms the method is forgiving and robust in the violation of assumptions, especially in comparison with time point-counts. Indeed, distance sampling has become the method of choice for estimating density since about 1990 (Bibby et al. 1998, 2000).

Finally, simple presence or presence-absence methods are perhaps the easiest methodology to understand and implement (e.g., Engler et al. 2004). Presence methods count species registrations rather than individuals per species as registrations. Moreover, observations are necessarily limited to timed observation periods or specific observation points or transects. Clearly this data is not very useful for estimates of abundance (e.g., Norvell et al. 2003), but it can be quite good for estimating seasonal abundance and in the short run provides a better estimate of richness than many other methods (Bibby et al. 1998).

**Methods Chosen for Surveys at Camp Swift**

Our selection of methods was constrained by the need to observe all bird species present at Camp Swift and by the difficulty in getting around Camp Swift given the highly

variable quality of roads (and road maintenance) within the base. Because of the large size of Camp Swift, early in the survey process we made several decisions to focus our research time most effectively. First, we decided to avoid creating transects in the most-disturbed habitats and to limit the number of transects within the live firing range (Figure 5–1). Second, we divided Camp Swift into five regions. These regions are characterized more by proximity and driving convenience than by any conscious effort by us to divide Camp Swift into a meaningful subsection of ecotypes beforehand and are thus not described here in detail or shown on Figure 5–1. Each visit to Camp Swift would normally include a visit to only one region. We tried to keep this rule consistent, though poor road conditions occasionally prevented us from reaching some portions of Camp Swift, often for a several weeks in a row, forcing us to survey transects on the basis of their accessibility rather than region.

We settled on a combination of distance sampling (based on point-transects) and simple presence when between timed distance sampling surveys. Given our budget constraints, a minimum of three visits per month spaced at least one week apart per visit was deemed sufficient to provide good richness and abundance resolution and balance our budget limitations.

Classic distance sampling methodology creates a random grid imposed on a landscape to define transects. This method seemed impractical given the scale and accessibility issues mentioned above (not to mention the extremely dense undergrowth in some areas). Moreover, the time to reach many of the transects generated by a random grid would reduce the number of transects we could effectively conduct given the additional amount of time required to get to and from each trailhead. Instead, we felt that the network of old and largely unused roads could substitute for a random grid. We therefore chose to depend largely on these old roads for our transects. Note that our

transects were not absolutely straight as a result but tended to veer with the roads. We tried to limit this deviation as much as possible, though some curvature can be seen on transects 10 and 16 (Figure 5–1).

Another significant compromise we made was to focus on morning transect runs, a sampling period that would give us the best trip to trip comparison and the period when most species are active, particularly species that are in decline, threatened, or endangered. We surveyed Camp Swift only once at night during the study period (15 August 2004), which decreased our power to estimate owls and nightjars and a few other groups. We felt that this compromise was reasonable because the ability to detect birds would be much more difficult in the evening, particularly along transects.

**Training, Preparation, and Organization**

October 2003 was spent hiring and training staff and laying out transects. We first laid out 16 transects (Figure 5–1), which necessitated substantial work in clearing and marking paths. Each transect measured between 280 and 520 meters in length, with all but two transects spanning either 400 or 440 meters. All transects consisted of pause points every 40 meters (estimated with a handheld GPS unit); transects running in parallel stood at least 150 meters apart. In most cases, the transects were much farther from one another. In one case, we used opposite ends of a single road with different habitat types at either end (transects 6 and 7), though in this case we never sampled both transects on the same day.

Our protocols stated that a team of observers would wait at least 90 seconds at a pause point (but longer if activity levels required more time to identify and record data), with one designated "lister" to record species, the number of individuals, the radial degrees from north, and the radial distance from observer (the latter two categories of

data are used by Distance to calculate the detectability curve). For simplicity, a pause point and its following 40 meters of transect were considered a single observation unit. When a bird was spotted visually, an electronic rangefinder provided +/- 0.5 meter accuracy, and field training for our staff included estimating distance for aural registrations. There was no maximum detection distance limit ("stratification" in the language of distance sampling) placed on observers. The 90-second wait at a point could be longer if there were many registrations at a point, and occasionally pauses lasted up to 5 minutes. Species could also be recorded while walking at a normal pace between points along a transect, though these proved to be far fewer than at the pause points. On some winter days with little bird activity, a transect might take only 35 minutes to walk. A busy high-activity day might require 65 minutes. So-called pishing was prohibited on transect because of its potential to violate assumptions regarding the detection of individual birds.

Each trip to Camp Swift included a collection of presence data upon entering the base and between transect runs, with distance sampling of between one and four transects. Some regions received more attention than others as a result of the higher quality roads between these regions and various entrances. Moreover, only a handful of our senior team leaders actually learned their way around Camp Swift, even with maps we made for this purpose. Thus, our transects varied between three and nine samples (mean: 6.2 samples) depending on familiarity with a particular transect and its accessibility.

Steady precipitation could cancel a trip, as could fewer than two spotters able to make a trip on a particular date. Trips were scheduled to be begin within 30 minutes after sunrise, requiring us to leave Austin quite early in the morning. As we reached the eastern city limits of Elgin, we would call one of two master sergeants at the base to alert them to our imminent arrival, determine if any new regions were designated hot (live

fire) zones, and provide an estimate of our exit time and exit gate. Upon quitting Camp Swift, the master sergeant was called again to alert him of our departure through a particular gate. These procedures were followed rigorously.

Observers fell into three categories: senior team leaders, team leaders, and spotters (Supplement 2). Each transect run had to have at least one team leader or senior team leader in attendance as they had the highest skill levels and experience. Spotters could be intermediate rather than advanced birders. Senior team leaders differed primarily in supplemental tasks, such as organizing trips, driving, and performing transect, equipment, and vehicle maintenance.

We knew that the quality of the data depended on the ability of our observers to accurately identify species and estimate distances and angles. Therefore, we created regular systems to review bird songs from recent visits in a series of audio CDs with tailored mixes of commercial bird vocalizations, and all observers were included in a project listserv that noted significant new species that had been seen to guide personal study. We also trained observers in the field and off site at Brackenridge Field Laboratory to estimate distance by sight and sound and in the use of electronic range finders. The use of multiperson teams also proved to generate on-transect discussion to confirm vocalization identification and angle and distance. When in doubt, at least one person per trip brought an Apple iPod with a full list of commercial vocalizations for the lower 48 states for field confirmation of unclear identifications, which was particularly useful for groups such as flycatchers or the chip notes of warblers and sparrows. In a handful of cases, we eventually assumed that partial identifications of a few species would have a default identification: Tufted titmouse (*Baeolophus bicolor*[3]) rather than Black-crested

[3] The first appearance of a species in this report will include the common name and the scientific name. Subsequent appearances of this species will only have the common name. A complete listing of species found at Camp Swift with scientific and common names is provided in Supplement 1.

titmouse (*B. atricritatus*), Ruby-throated hummingbird (*Archilocus colubris*) rather than Black-chinned hummingbird (*A. alexandri*). Notably, we did register a handful of Black-crested titmice but no Black-chinned hummingbirds. Otherwise, we asked observers not to record registrations unless they were "very sure" of the identification. If unsure, they were to take angle and distance data, systematically describe song/visual features, and narrow the identification to family or genus. In a few cases, these IDs never got beyond (for instance) "swallow species," but most were ultimately resolved off-transect. Unresolved registrations (numbering less than 20 out of some 3450) were excised from the data analysis.

**Data Processing and Analysis**

Distance sampling is based on the assumption that the ability to detect an organism declines in a predictable way from the point or transect (Bibby et al. 1988, Buckland et al. 2001, 2004). Hence, the distance from the observer and angle relative to the transect are crucial data to include with each registration, and Distance 4 can use this data to determine the perpendicular distance of the observed organism to the transect (Thomas et al. 2004). By fitting curves to the spatial distribution of registrations (based on perpendicular distances), Distance uses the Aikake Information Criterion (AIC) to choose between a variety of distribution models (Buckland et al. 2001, Thomas et al. 2004). In the event that no one model can provide a satisfactory fit to the data, some categories can be removed if grounds exist for believing that there may have been a sampling bias. For instance, American crows (*Corvus brachyrhynchos*) produce very loud vocalizations, with calls that can be heard for hundreds of meters, and we estimated a handful of Pileated woodpecker (*Dryocopus pileatus)* calls at 500 meters. We found in most cases, however, that the ability to estimate distances over 150 meters was less accurate than

distances under 150. The truncation of the farthest calls usually provided a good AIC fit. Likewise, some species normally seen in flight such as Chimney swifts (*Chaetura pelagica*) and Barn swallows (*Hirundo rustica*) often registered as 0 degrees and 0 meters, as they were regularly observed directly overhead. These detections also created a very uneven spatial distribution curve and probably overestimated the density of these species (Bibby et al. 1998, Buckland et al. 2001). Distance also allows for the removal of data within a given distance of the transect in such cases, and for both species the reduction of observations within 20 meters of transects provided a satisfactory AIC fit.

The effect of these manipulations on the quality of data analysis should be small. Indeed, observers are human, and the tendency to regularize distances to birds that are very near or very far seems quite natural even when consciously trying to avoid such difficulties. The worst error that may result from modifying the data actually used to generate species densities is that the resulting estimate may be somewhat low. However, we believe that our estimates have been made with sound assumptions, and that the results largely fit our experiences and perceptions as field biologists in central Texas.

The greatest weakness of distance sampling may be the need for enough registrations to make a good estimate of species density — the degree of statistical power, in other words. An informal survey by Matthews of biologists using Distance suggested that 30 registrations per species was a good rule of thumb for making a reasonable estimate of density. We found that in some cases Distance could make estimates with as few as a nine or 10 registrations, though the number of cases in which Distance warned of constraints on parameters while fitting curves increased dramatically below 20 registrations per species. Indeed, some curves could not be matched and these are reported as is.

The most difficult cases to evaluate via distance sampling, however, were species with the fewest registrations. Here, these species will be defined as less than 10 registrations, with many species that had only one or two registrations. Note too that *registration* refers not just to the number of individual birds; a single of flock of birds is a one registration. Thus, some species with a relatively large number of birds counted — such as Cattle egrets (*Bubulcus ibis)* — were seen in only a handful of flocks. Many of the colonial waterbirds fell into this category, including Double-crested cormorants (*Phalacrocorax auritus)* and Long-billed curlews (*Numenius americanus)*[4]. Indeed, distance sampling is not alone in this regard. These species may have been registered so seldom for a variety of reasons, such as rarity in this (or any) portion of their range, great difficulty in detecting individuals either aurally or visually, and activity periods different than the sampling period (as with owls and nightjars). For endangered and threatened species, the first two of these three categories are most relevant. Unfortunately, little can be firmly concluded about the least-seen species in this study without additional work on individual species.

The entry and analysis of presence data was relatively straightforward compared to the distance sampling data. Presence data as we collected it essentially showed the number of trips in which a species was observed. The maximum number of registrations, therefore, was equal to the maximum number of trips, or 43. This gives the rank abundance data a much flatter appearance than the distance sampling data.

## RESULTS, ANALYSIS, AND SURVEY METHOD COMPARISON

Camp Swift was surveyed over 43 trips for presence data and 41 trips for distance sampling. One hundred transect surveys were conducted via distance sampling,

[4] This issue with Long-billed curlews is particularly significant given the species's status as a Partners in Flight type I species of concern. See also Supplement 3.

producing 3452 registrations, which consisted of 4742 individual birds.[5] Presence methods resulted in a total of 4094 registrations. The latter data set spanned from 15 October 2003 to 18 November 2004,[6] while distance data ranged between 5 November 2003 and 13 October 2004.

**Species Richness**

A total of 133 species were observed during the study period at Camp Swift. Of this total, 111 species (83 percent) were registered by both presence methods and distance sampling (Supplement 1). These percentages appear quite comparable, but they belie other more subtle differences, with 22 species (17 percent) seen by either one method or the other. All of the species that were seen by only one method were rare species (that is, less than 6 registrations and not necessarily rare in a global sense) or species seen in one or two flocks (which often contain several dozen individual birds). In the case of the rare species, the overwhelming majority of these had only one or two registrations. No discernable patterns were observed regarding genus, family, or habitat preference for their observation by only one survey method. Most can be classified as migrants. A few (e.g., Pyrrholuxia, *Cardinalis sinuatis*) are best described as vagrants or near the edge of their range of highest abundance.

Given that the numbers of rare species observed by only one method are quite comparable, it must be assumed that each method was reasonably equivalent in observing species at Camp Swift that are present for only brief periods of time and/or are very cryptic. A corollary conclusion is that any registration of a rare species is a significant

[5] Again note that a registration is a single observation, which may include a flock of birds. Thus, in most cases a registration refers to a single bird but can include a group of dozens of geese, for instance.
[6] Data collected previous to the official start date was used for training purposes rather than analytical methods.

event, and that new species will be added as the study period lengthens and/or sampling frequency increases. Indeed, we added two new species on the last trip to Camp Swift.

This perspective is strengthened when considering Spearman's rank coefficient ($r_s$, which can range from 1 to -1) for the two methods in comparison with one another and to total species richness (Figure 5–2). The correlation between presence and distance sampling is weak (0.30), though the correlation between the combined data and distance sampling is very high (0.97) and much closer than the correlation between the combined data set and the presence data (0.82). This difference is reasonable given that most of the registrations in the combined dataset are from distance sampling rather than presence methods. The estimate of relative abundance is also significantly different between the two methods: presence and distance sampling have essentially no correlation in what each found to be the most abundant 25 percent of species observed, and only a 0.67 correlation for the most abundance 50 percent of species.

| | Presence–distance sampling | Combined–presence | Combined Methods |
|---|---|---|---|
| All species | 0.30 | 0.82 | 0.97 |
| Most abundant 25 percent of species observed | -0.08 | 0.12 | 0.95 |
| Most abundant 50 percent of species observed | 0.67 | 0.54 | 0.96 |

Figure 5–2. Spearman's rank coefficient of presence and distance sampling and combined avian richness data at Camp Swift

The two methods also differ in how they accrued new species (Figure 5–3). The combined dataset and the transect data show fairly even growth throughout the study period, reaching their midpoint of 50 percent of the final richness by early or mid February. Presence data reached its midpoint in late March, more than a month later. All

three datasets show a noticeable bump in the accrual of new species in late April and May, when the bulk of spring Neotropical migrants are passing through.

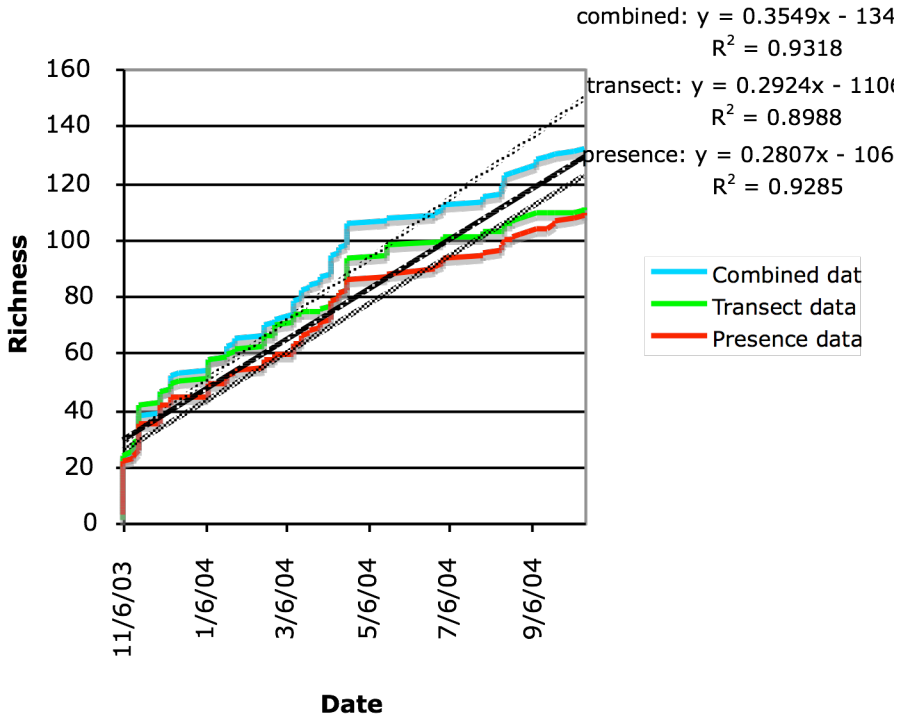



Figure 5–3. Richness survey methods comparison at Camp Swift.

**Abundance**

There are a number of methods to explore the species abundance data. One of the most traditional is via rank abundance charts (Figures 5–4 and 5–5), which show the number of registrations per species across the X axis, with the number of species corresponding to these registrations along the Y axis; other types of rank-abundance charts are also in common use (see Case 1999). Both presence and distance sampling methodologies show similar trends, with many "rare" species (that is, species with only a handful of registrations over the sampling period, concentrated on the lefthand side of the chart) and

a relatively small number of common species (concentrated on the righthand side of the chart). The presence data is flatter than the distance sampling data, while the latter approaches something closer to a classic "hollow ball" distribution (Magurran 2003).

There are a number of reasons for these differences. Perhaps the most basic reflects the fewer maximum number of presence registrations possible for any given species, with that maximum equal to the total number of trips. In contrast, the upper limit for registrations using distance sampling is theoretically unlimited. With both methods, the minimum number of registrations is, of course, one. There are far more rare species represented by distance sampling than by presence methods, and the relative distance between common and rare species is much greater. Magurran (2003) suggest that the distance sampling data is more typical for many types of complex communities and thus more accurate (e.g., Case 1999, Ricklefs 2000). Further, the distance sampling data matches our experiences in the field far more closely than the presence data.

In particular, the presence data tends to overrepresent species that are resident for long periods at Camp Swift and that are territorial. Thus, we probably overcounted a single Greater roadrunner (*Geococcyx californianus*) that had established a territory near gate 9, one of our frequently used entrance sites. Standard presence methodology does not compensate for multiple observations of the same individual. Thus, Greater roadrunners are ranked rather high in abundance with presence methods and more appropriately at a low density using distance sampling.

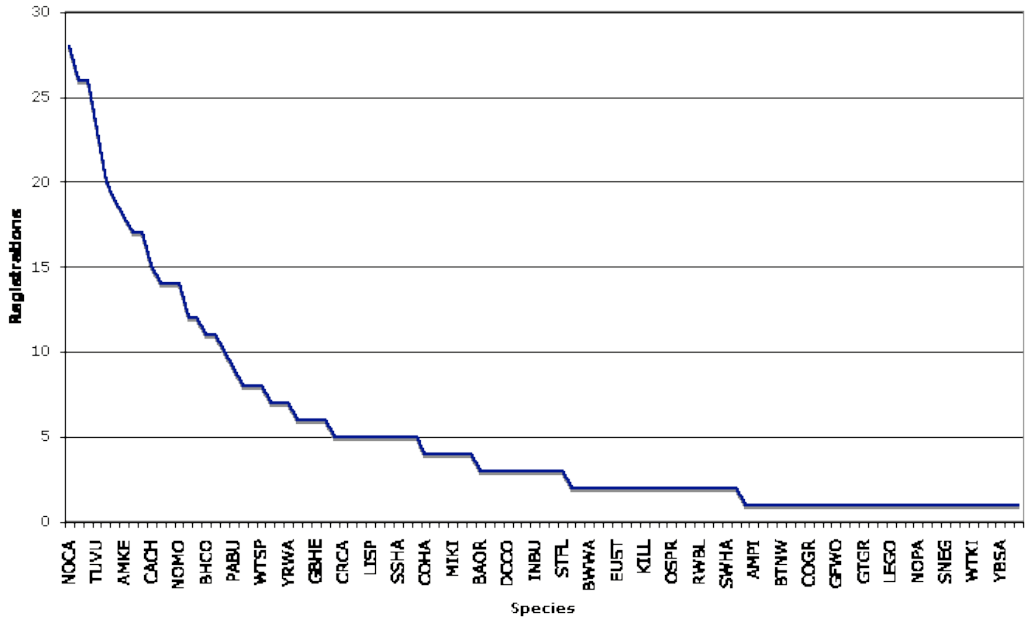



Figure 5–4. Rank abundance of presence data from Camp Swift.

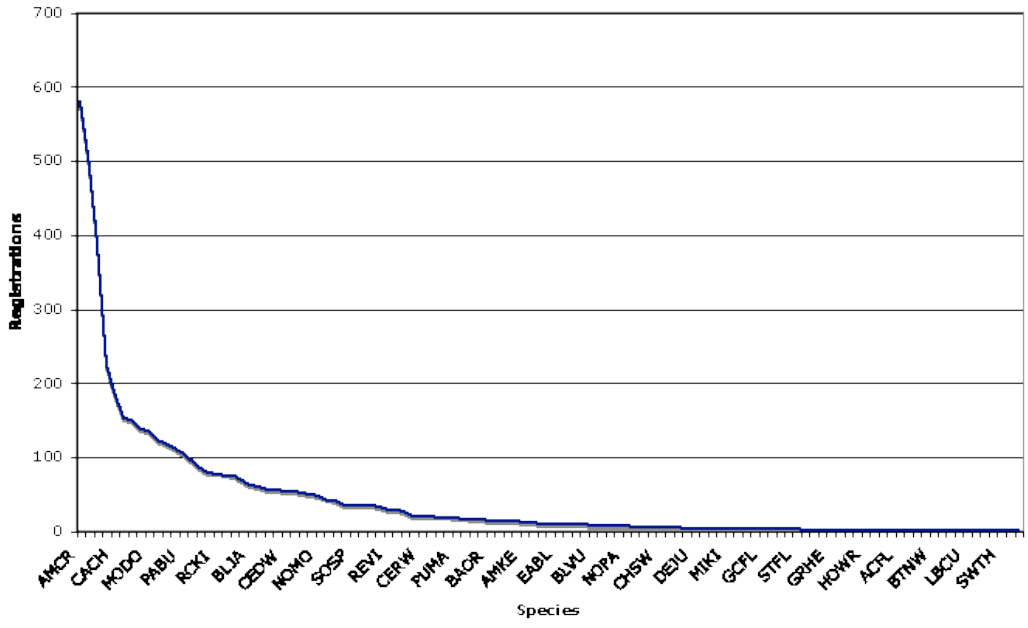



Figure 5–5. Rank abundance of distance sampling data from Camp Swift.

## THE ECOLOGICAL PLACEMENT OF CAMP SWIFT: CHARACTERIZING THE COMMUNITY

In terms of its bird community, Camp Swift lies near the conjunction of a number of different physiographic and ecological zones that influence its composition. Camp Swift lies roughly east of the line roughly demarking eastern from western North American species, and eastern species of plants and birds tend to dominate. Given the physiographic areas of Texas defined by Partners in Flight (PIF), Camp Swift can also be described as lying near the western edge of the Oaks and Prairies physiographic area. When eastern and western analogues tend to co-occur in this area, the eastern variety tends to dominate. Both Black-crested and Tufted titmouses (western and eastern species, respectively) are found at Camp Swift, but the Tufted titmouses far outnumber the Black-crested. This ratio is reversed in Travis county to the west, and Tufted titmouses are extremely rare just a bit farther to west of Travis county. In contrast, in counties farther east than Camp Swift, Black-crested titmouses are extremely rare (Lockwood and Freeman 2004). Other examples include the eastern yellow-shafted morph of the Northern flicker (*Colaptes auratus*), which is found almost exclusively at Camp Swift rather than the western red-shafted morph (though a vagrant of the latter was seen on once occasion). From a habitat perspective, the substitution of eastern red cedar (*Juniperous virginiana)* for Ashe juniper (*Juniper ashei*) is probably significant to a wide range of animal species. Numerous other examples could be provided along these lines (detailed floral examples are documented in Damude et al. 2005).

Camp Swift's biota is also clearly a rural and nonurban environment. Few urbanized Texas species are found: White-winged doves (observed in low numbers; *Zenaida asiatica,* native with a boom in urban populations over the twentieth century), Rock pigeons (not observed; *Columba livia,* Eurasian in origin), House sparrows (observed only once, and in the most urbanized habitat at Camp Swift; *Passer*

*domesticus,* Eurasian in origin), and Great-tailed grackles (observed only a handful of times; *Quiscalus mexicanus,* Central American in origin with a dramatic twentieth-century range expansion). In contrast, on surveys at Camp Mabry in Austin, Texas, the same survey teams found that counting these super-numerous species interfered with the registration of other species occurring at lower densities. While these four species may constitute 20 percent of the avifauna biomass of Camp Mabry and the greater Austin area, they constituted much less than 1 percent of the richness at Camp Swift. The status of Camp Swift as a nonurban habitat is likely to increase in importance as its environs become increasingly urbanized.

Given this background, the habitat types can be lumped into several broad categories: closed-canopy forest (most often oak-hickory or oak-redcedar, but one point on transect 16 includes pine forest), open-canopy oldfields, oak savannah and scrublands, and riparian areas.[7] Each transect was designated after the end of the survey period into one of these four types based on 75 percent or more of the points in the transect falling into a particular category (Table 5–1). Riparian areas make up a tiny proportion of the habitat at Camp Swift in terms of area (perhaps 5 percent?). Most of the intact portions of Camp Swift are closed-canopy forest, with perhaps 10 to 20 percent of the surface area in open oldfields and at least another 20 percent savannah and scrublands.

In turn, after aggregating transect data by category these habitat types display distinct patterns of diversity (Table 5–2). Open oldfields and closed-canopy forest show very similar densities of birds despite forest transects having on average less than half as many registrations as oldfields and about half as many species. The mix of species between these two types is also quite different, with sparrows and other seed-eating species far more common in the oldfields. Given the higher number of registrations, why

[7] Detailed plant descriptions of each habitat are included in Damude et al. 2005.

is the density of birds identical in these two habitats? Perhaps the most parsimonious answer is that birds are far more detectable in open meadows than in shrubby and dark forests. The larger number of registrations corresponds to a higher detectability coefficient in Distance.

In contrast, the savannah/scrublands and riparian areas are far more similar to one another than to the open oldfields and closed-canopy forest (Table 5–2). Their richness measures are almost identical (though again they have different mixes of species from each other and from the other two habitat types), their mean number of registrations are almost the same (about 47 to 49 per trip), and their mean densities are far higher than the oldfields and forests, perhaps reflecting their relatively higher rates of disturbance (e.g., burns, floods). These habitats tended to concentrate many migrants, especially warblers and vireonids, with sparrows also relatively common in the grass-rich scrublands and savannah. The especially high density of birds in riparian areas suggests that these regions have a significance in terms of habitat far in excess of their relative area.

| Transect | Percentage of total regis-trations | Percentage of total birds observed | Percentage of total species richness[8] | Estimated density of birds/hectare | Habitat type |
|---|---|---|---|---|---|
| **1** | 7.8% | 9.7% | 48.65% | 1.98 | open |
| **2** | 7.1 | 7.4 | 43.24 | 1.33 | open |
| **3** | 5.2 | 4.2 | 25.23 | 1.01 | canopy |
| **4** | 6.4 | 5.6 | 33.33 | 2.53 | canopy |
| **5** | 3.7 | 3.5 | 21.62 | 4.40 | savannah |
| **6** | 6.2 | 6.0 | 34.23 | 3.93 | riparian (pond) |
| **7** | 4.2 | 3.3 | 25.23 | 6.04 | riparian (stream) |
| **8** | 6.1 | 7.7 | 41.44 | 2.41 | riparian (stream) |
| **9** | 6.9 | 6.2 | 41.44 | 3.71 | scrub |
| **10** | 2.6 | 2.1 | 23.42 | 1.05 | canopy |
| **11** | 5.6 | 4.4 | 32.43 | 1.31 | canopy |
| **12** | 8.8 | 12.4 | 52.25 | 1.12 | open |
| **13** | 6.0 | 5.5 | 36.94 | 1.87 | canopy |

[8] Richness here is defined as the total number of species observed via distance sampling methodology, or 111 species versus the combined total of 133.

| | | | | | |
|---|---|---|---|---|---|
| **14** | 4.4 | 4.2 | 26.13 | 1.48 | canopy |
| **15** | 8.0 | 6.8 | 36.04 | 3.10 | savannah |
| **16** | 11.0 | 11.0 | 45.95 | 1.74 | open |
| **Mean** | 6.3 | 6.3 | 35.5 | | |

Table 5–1. Habitat characteristics of avian transects at Camp Swift, Texas.

| | **Mean richness** | **Mean registrations** | **Mean density** |
|---|---|---|---|
| **Canopy** | 29.58 | 31.92 | 1.54 |
| **Open** | 47.52 | 75.71 | 1.54 |
| **Savannah/scrub** | 33.03 | 47.56 | 3.74 |
| **Riparian** | 33.63 | 49.28 | 4.13 |

Table 5–2. Broad traits associated with habitat types, Camp Swift, Texas.

## Endangered and Threatened Species

Three major agencies relevant to this study publish large-scale recommendations on species of particular risk of extinction: the U.S. Fish and Wildlife Service, Texas Parks and Wildlife, and Partners in Flight (PIF). These groups often work with the same bodies of data, though they may analyze and interpret this data in contrasting ways.

PIF is a nongovernmental organization that works very closely with other NGOs and federal, state, and local conservation and wildlife management authorities in evaluating the status of North American avian populations and species. Of these three groups, PIF is the only organization that (a) focuses exclusively on birds and (b) evaluates trends by defined physiographic areas and by conservation regions (Carter et al. 2000).

No species listed by state or federal authorities as endangered were found at Camp Swift. However, eight species receiving PIF's highest ranking for overall concern

were found in addition to two species (Black-chinned hummingbird and Swainson's warbler) at the same ranking from MAPS data (Table 5–3, Supplement 3).

| **Common name** | **Scientific name** |
|---|---|
| American Woodcock | *Scolopax minor* |
| Chuck-will's-widow | *Caprimulgus carolinensis* |
| Field Sparrow | *Spizella pusilla* |
| Harris's Sparrow | *Zonotrichia querula* |
| Kentucky Warbler | *Oporornis formosus* |
| Loggerhead Shrike | *Lanius ludovicianus* |
| Long-billed Curlew | *Numenius americanus* |
| Painted Bunting | *Passerina ciris* |
| Scissor-tailed Flycatcher | *Tyrannus forficatus* |
| Black-chinned Hummingbird[9] | *Archilocus alexandri* |
| Swainson's Warbler[10] | *Limnothlypis swainsonii* |

Table 5–3. Species receiving a PIF highest overall concern ranking found at Camp Swift, Texas

Species cited by PIF at other levels of concern are included in Supplement 3, as well as species described as regionally of concern but not found at Camp Swift. Of the species we observed that are listed in Table 5–3, only Harris's sparrow, Kentucky warbler, and Long-billed curlew can be described as rare according to our methods, but the first two of these three are quite cryptic in their habitats, and their presence warrants further focused investigation. Many sparrows, for instance, cannot be accurately surveyed without mistnets or lines of spotters walking across fields to stir up hiding birds. Kentucky warblers are often found in lowland habitats, especially riparian areas, and we only surveyed three such transects. Long-billed curlew are relatively large birds but quite shy and most often observed in migration in east-central Texas, though many are resident year-round (Lockwood and Freeman 2004). They too may require more focused survey methods.

[9] From MAPS data.

**Diversity and Abundance Hotspots**

The citation of areas that have higher avian diversity is based strictly on transect data, which is the only geographic means of constraining registrations at Camp Swift (Table 5–4, Figure 5–1). Transects varied in their total number of registrations from 93 to 389. The number of samples per transects ranged between 3 and 9, with a mean of 6. Once the number of registrations was normalized for the number of times a transect was run or sampled, several interesting patterns emerge.

| Transect | Times run | Registrations | Total birds | Normalized by trips | Richness | Density | Habitat |
|---|---|---|---|---|---|---|---|
| 1 | 5 | 277 | 462 | 92.40 | 54 | 1.98 | open |
| 2 | 6 | 250 | 352 | 58.67 | 48 | 1.33 | open |
| 3 | 9 | 182 | 201 | 22.33 | 28 | 1.01 | canopy |
| 4 | 8 | 225 | 264 | 33.00 | 37 | 2.53 | canopy |
| 5 | 3 | 129 | 164 | 54.67 | 24 | 4.40 | savannah |
| 6 | 6 | 220 | 284 | 47.33 | 38 | 3.93 | pond |
| 7 | 4 | 147 | 158 | 39.50 | 28 | 6.04 | stream |
| 8 | 6 | 214 | 366 | 61.00 | 46 | 2.41 | stream |
| 9 | 7 | 245 | 294 | 42.00 | 46 | 3.71 | scrub |
| 10 | 4 | 93 | 98 | 24.50 | 26 | 1.05 | canopy |
| 11 | 8 | 199 | 211 | 26.38 | 36 | 1.31 | canopy |
| 12 | 9 | 312 | 586 | 65.11 | 58 | 1.12 | open |
| 13 | 5 | 213 | 260 | 52.00 | 41 | 1.87 | canopy |
| 14 | 6 | 155 | 200 | 33.33 | 29 | 1.48 | canopy |
| 15 | 7 | 282 | 322 | 46.00 | 40 | 3.10 | savannah |
| 16 | 6 | 389 | 520 | 86.67 | 51 | 1.74 | open |
| **Mean** | 6.2 | 220.8 | 296.4 | | 49.1 | | |

Table 5–4. Transect diversity and abundance traits, Camp Swift, Texas

First, there is a zone with higher bird density in the eastern portion of Camp Swift (transects 4 through 7); a second such zone may exist in the south-central region as well (transects 8 and 9). The eastern zone of high bird density spans a number of different habitat types. However, species richness is not exceptionally high (and indeed never goes

[10] From MAPS data.

above the mean richness for Camp Swift). Thus, there are many birds in this region, just not many kinds of birds.

Second, species richness is always above the mean (and reaches its highest overall levels) in the open oldfield habitats (transects 1, 2, 12, and 16). In contrast to transects 4 through 9, however, the mean density of birds is relatively low while the richness is high (Table 5–2). Thus, in open environments there are many kinds of birds, just not many of them.

**Diversity by Time: Critical Periods**

Diversity levels made a steep climb regardless of presence or distance sampling during the spring migration period of late April and early May (Figure 5–3). A similar but smaller climb in fall 2003 corresponds to the fall southern migration in September through early November. There is an interesting dead zone, however, in January through mid February, when many transects reached their richness and abundance nadir; several transects during this period showed less than 10 registrations over their whole length. These low points may reflect mid-winter habitat shifts or a reduction in actions that make individuals more detectable, such as vocalizations or foraging in groundcover. We can see these patterns to some degree by comparing registrations for a resident species (Carolina wren, *Thryothorus ludovicianus)* and a migrant species (Ruby-crowned kinglet, *Regulus calendulus).*

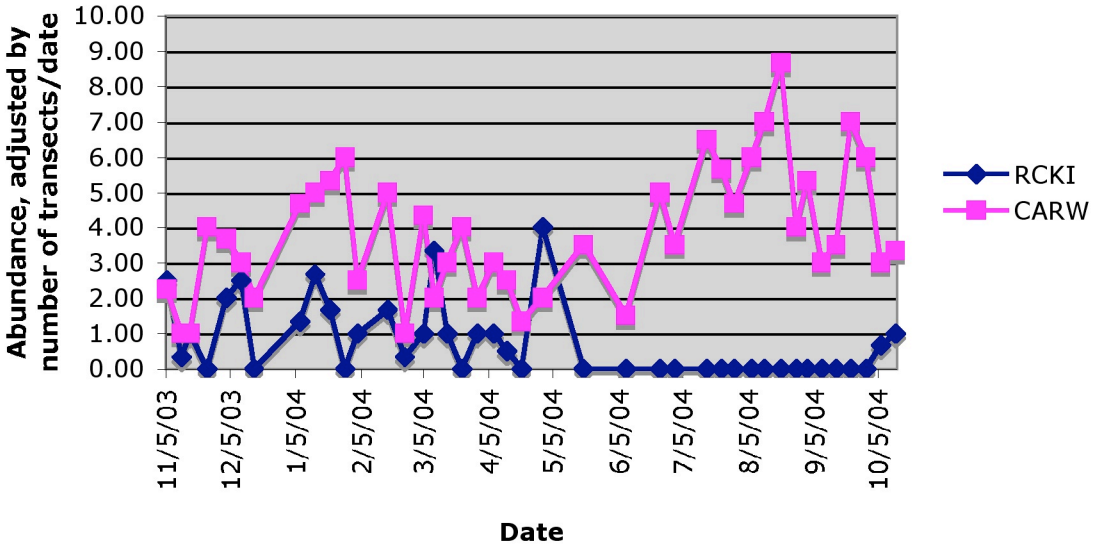
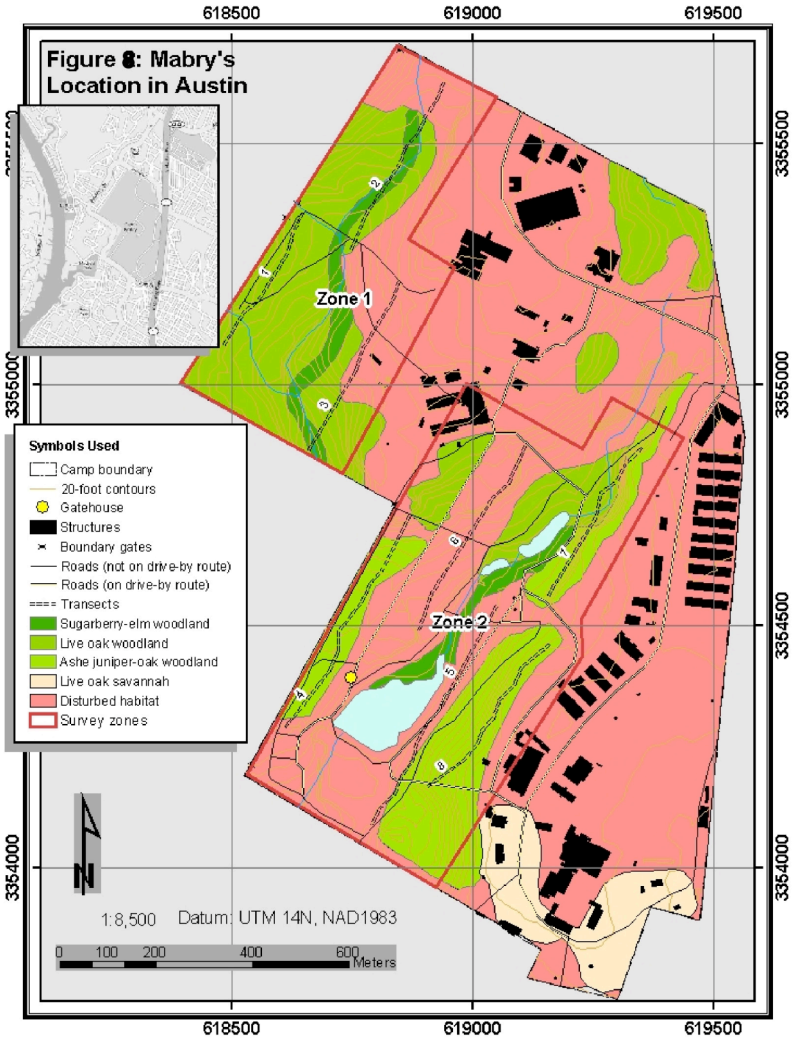



Figure 5–6. Abundance through time at Camp Swift over the survey period for Ruby-crowned kinglets and Carolina wrens.

Figure 5–6 shows clearly the overwintering season for Ruby-crowned kinglets, including the fall and spring bursts of abundance when many individuals are on the move between the overwintering and breeding regions. Likewise, Carolina wrens remain relatively constant over the course of the year in keeping with their resident status; much of the variation in abundance probably results from increased periods of detectability rather than sudden increases or decreases of individual birds. Such changes could results from territory establishment, cryptic brooding female behavior, and temporary shifts in foraging behavior.

These species may serve as good conservation proxies for less abundant species in their seasonal changes. If either of these species were of concern, the critical periods (generally speaking) for residents would be their breeding season, which extends into summer for Carolina wrens. For overwintering species, however, the period of concern is probably the period just before the onset of spring migration, a period likely to have a large impact on breeding success.




Figures 5–7 and 5–8. Survey region and physiographic context of Camp Mabry and Camp Mabry's location within the city of Austin (inset of Figure 5–7).

## CAMP MABRY SURVEYS

### Site Description

Between its founding in 1892 and as recently as the late 1930s, Camp Mabry was located at the urban-agricultural interface of northern Austin. Development has radically changed Camp Mabry's context since then as the city of Austin has moved beyond and enclosed the camp. Covering 145.9 hectares (360.5 acres), Camp Mabry is now one of the largest islands of least-developed land within the Austin metropolitan area (Figure 5–7). This is

not to suggest that Camp Mabry is pristine or more accurately reflects regional landscapes prior to European settlement. But human impacts on Camp Mabry have differed significantly from the rest of Austin since the founding of base. Indeed, past and current land-use differences continue to influence the diversity and abundance of bird species found there now and in its surrounding environs.

### *Zone 1*

The forested portions of Camp Mabry fall into roughly two zones defined by Matthews. Zone 1 is the northwestern portion of Camp Mabry (Figure 5–7). Measuring 26.0 hectares (64.3 acres) or 18 percent of Camp Mabry, zone 1 is roughly bisected by a creek running northeast-southwest and by dirt roads that follow the northern, southern, and western edges. Another road splits the region into northern and southern halves, and a handful of intermittent small streams drain the larger creek. Zone 1 is bounded on the east by mown lawns, the high fence that outlines the southern and western property boundaries, and the parking lot that lies between the forest and northern property line. A wealthy single-family residential neighborhood buffers the western, southern, and northern edges of zone 1 with large yards containing bird feeders and large trees with cover and forage for insectivorous birds. No doubt these yards also tend to baffle urban sounds and reduce aural disturbance from these directions than other portions of Camp Mabry, which are not surrounded by such neighborhoods (Figure 5–8). From a habitat-centered perspective, these properties effectively increase the size of zone 1 and make this portion of Austin more appealing to birds.

There is much variation in vegetation in zone 1 (see Damude et al. 2005 for a detailed analysis and report). The southeastern corner of zone 1 is the highest elevation at Camp Mabry, with many invasive exotic trees (e.g., Chinaberry [*Melia azedarach*])-*Ashe*

*juns are native and only invasive due to poor soil management and lack of fire*. Most of the rest of zone 1 consists of juniper-hardwood forest, dominated by mature oaks (*Quercus* spp.), cedar elms (*Ulmus* spp.), and pecans (*Carya* spp.). Nonnative shrub and tree species are found in the neighboring residential area, and some of these have seeded offspring in zone 1.

Not all of zone 1 is forested. Several small grassy and shrubby areas are interspersed throughout the zone, particularly along the roads. A tongue of mown lawn extends from the center of zone 1 to the northeast. One telephone line right of way runs east-west through the northern third. And some much younger and more shrubby thickets border the eastern edge of the zone.

We don't know the history of the use of this area by the National Guard, but during the study period zone 1 saw intermittent use for field exercises, mostly via foot traffic. Much of this traffic was also concentrated during weekends (no surveys were conducted on weekends). Such disturbances probably had low impacts as far as bird species were concerned, though these exercises seemed to involve removing much of our transect-marking tape.

Higher-impact disturbance was also observed in this zone during the same period, however. The northern portion of region 1 appears to be used primarily by foot traffic rather than vehicles, particularly for field training. Approximately 10 acres of land were cleared of oaks during November and December 2003 in the northwestern corner of zone 1 to control an infestation of oak wilt. No transects were conducted in this area while harvesting was underway.

### *Zone 2*

The second zone stands to the southeast of zone 1 and extends from the strip of land just west of the current entrance road to the large group of older buildings in the southeastern quadrant of Camp Mabry (Figure 5–7). The northern and eastern edges are largely defined by the main road. The southern boundary is a high fence separating zone 2 from 38th Street. A creek runs north-south through zone 2, draining into a small pond, which flows into a creek again and then enters a larger pond. Paved and unpaved roads segment much of the center of zone 2, with most of these running north-south. A large mown lawn in the center of zone 2 was often used for training and recreation purposes during the study period, and a second large lawn is located between the larger pond and 38th Street.

Broadly speaking, zone 2 is a shallow canyon. The creek and ponds act as riparian corridors; they often contained quite different bird species than other portions of Camp Mabry at any given time. A bunker (just north of transect 5) is used for munitions storage.

Water sources in zone 2 were generally more permanent during the study period than in zone 1. Both ponds have been in existence for several decades, and the main creek in the zone seemed less-intermittent and more regular in its flow patterns than the main creek in zone 1, though these observations were not quantified. What is clear is that elevations in region 2 are generally lower, with more riparian habitat. Between the two ponds and in the northeastern canyon traced by transect 7, there are patches of hardwood bottomland forest. Along the creek and ponds, canopies are generally tall and closed, with less shrubby and more hardwood growth.

Regular long-term sources of disturbance probably afflict zone 2 more than zone 1. Mo-Pac (Loop 1) auto and train traffic are much closer to zone 2, and busy roads within the camp surround three sides of the region (Figures 5–7 and 5–8). The many

roads within zone 2 are also among the most used in Camp Mabry, especially during the morning and evening rush hours. Extensive foot traffic was also seen during the study period, including training and recreational activities in the central mown lawn. Episodic sources of disturbance during the study period — often lasting weeks or months — included the construction of the new entrance gate, the modification of a drainage ditch from the eastern side of Camp Mabry to zone 2's creek, and the repair of the bridge between the drainage ditch and the upper pond.

Our perception of disturbance in zone 2 was that low-level foot traffic was much higher than in zone 1, vehicular traffic was many times higher, and significant construction during the study period affected zone 2 far in excess of zone 1.

For instance, the large mown lawn between the southern pond and 38th Street was converted into large mounds of soil beginning in the late fall and early winter of 2003–04, thereby losing much of its value as bird habitat. Other most notable changes have been near the entrance road and between the entrance road and the western property boundary (the "strip," containing transect 4; Figure 5–7). The latter's fenceline road was also covered by large piles of soil and gravel at the beginning of the study period. Several hectares were also cleared in the strip for an east-west utility right-of-way. The construction of a new guard station on the entrance road created a lot of noise in this area and resulted in the loss of at least one hectare of forest edge habitat.

## METHODS CHOSEN FOR SURVEYS AT CAMP MABRY

Our basic survey methods followed those used at Camp Swift, described above. To ensure that our presence methods were more comparable between visits, we took advantage of the restricted entrance methods by creating a driving route used with almost no variation over the course of the study period, and this so-called "drive-by" trip on each

visit to Camp Mabry passed primarily through more-disturbed areas outside of zones 1 and 2, effectively passing within 150 meters of more than 80 percent of the non-transect regions of the base. This route totaled 5.1 km or 3.2 miles (Figure 5–7). Given our budget constraints, a minimum of three visits per month that were spaced at least one week apart per visit was deemed sufficient to provide good richness and abundance resolution.

One significant compromise we made was to focus on morning transect runs, a sampling period that would give us the best trip to trip comparison and the period when most species are active, particularly species that are in decline, threatened, or endangered. We did not survey Camp Mabry at night during the study period, which decreased our power to estimate owls and nightjars and a few other groups. We felt that this compromise was reasonable because the ability to detect birds would be much more difficult in the evening, particularly along transects.

**Training, Preparation, and Organization**

September and October of 2003 were spent hiring and training staff and laying out transects. Given the smaller size of Camp Mabry relative to Camp Swift and the high reliability of reaching each transect year-round, we were able to follow a more classic method of layout transect (following Bibby 1999). We settled on four transects per region, with each transect at least 400 meters in length and consisting of pause points every 40 meters. These were laid out on a north-south grid, with each transect at least 150 meters apart. In most cases, the transects were much farther from one another, with adjacent transects offset (Figure 5–7). As at Camp Swift, our protocols stated that a team of observers would wait at least 90 seconds at a pause point (longer if activity levels required more time to identify and record data), with one designated "lister" to record species, number of individuals, degrees from north, and distance from observer (the latter

two categories of data is used by Distance to calculate the detectability curve). For simplicity, a pause point and its following 40 meters of transect were considered a single observation unit. When a bird was spotted visually, an electronic rangefinder provided +/- 0.5 meter accuracy, and field training included estimating distance for aural registrations. There was no maximum detection distance limit ("stratification" in the language of distance sampling) placed on observers. The 90-second wait at a point could be longer if there were many registrations at a point, and occasionally pauses lasted up to 5 minutes. Species could also be recorded while walking at a normal pace between points along a transect, though these proved to be far fewer than at the pause points. On some winter days with little bird activity, a transect might take only 35 minutes to walk. A busy high-activity day might require up to 55 minutes. So-called pishing was prohibited on transect because of its potential to violate assumptions regarding the detection of individual birds.

Transects were numbered sequentially from east to west. Each trip to Camp Mabry included a drive-by and between one and four transects. For the first few months, these were selected by a random pattern generator, but we eventually opted for a nonrandom order, selecting one transect per portion of Camp Mabry to the east and west of the main entrance road in sequence, with the selected western transect numbered four higher than the eastern transect (thus, we might do transects 1 and 5 on one trip). Steady precipitation could cancel a trip, as could fewer than two spotters able to work. Trips were scheduled to be begin within 30 minutes after sunrise.

Spotter organization, training, and recording methods were identical to those of Camp Swift (see staff list in Supplement 2).

## RESULTS, ANALYSIS, AND SURVEY METHOD COMPARISON

Camp Mabry was surveyed over 43 trips. Eight-three transect surveys were conducted via distance sampling, producing 2729 registrations, which consisted of 3488 individual birds. Presence methods resulted in an additional 2721 registrations. Both data sets spanned from 20 September 2003 to 20 November 2004.[11]

### Species Richness

A total of 116 species were observed during the study period at Camp Mabry. Of this total, 95 species (82 percent) were registered via presence methods, and 99 species (85 percent) were registered by distance sampling (Supplement 5). These percentages are quite comparable, but they belie other more subtle differences. For instance, 17 species (15 percent) were observed by presence methods but not by distance sampling, and 21 species (18 percent) were observed by distance methods but not via presence. All of the species that were seen by one method only were rare species — that is, less than 6 registrations, and the overwhelming majority of these species had only one or two registrations. No discernable patterns were observed regarding genus, family, or habitat preference for their observation by only one survey method.

Given that the numbers of rare species observed by only one method are so comparable, it must be assumed that each method was reasonably equivalent in observing species at Camp Mabry that are present for only brief periods of time and/or are very cryptic. A corollary conclusion is that any registration of a rare species is a significant event, and that new species will be added as the study period lengthens and/or sampling frequency increases. Indeed, we added two new species on the last trip to Camp Mabry.

[11] Data collected previous to the official start date was used for training purposes rather than analytical methods.

This perspective is strengthened when considering Spearman's rank coefficient ($r_s$ = 1 to -1) for the two methods in comparison with one another (0.77) and to the total species richness (presence: 0.90, distance: 0.95). In contrast, the $r_s$ for the first 25 percent of the species observed shows a presence-distance correlation of -0.27, or essentially no correlation. Even when considering the first 50 percent of species, the $r_s$ is only 0.34.

Other data supports that the two methods differ in how they accrued new species (Figure 5–9). Presence observations resulted in a fairly steep addition of species before leveling off somewhat, reaching the midpoint of the final richness by trip 12, which was the 28th percentile of the total of 43 trips. Distance sampling accrued species more evenly over the study period and reached its richness midpoint by trip 21, though notable jumps occurred during the peak fall and spring migration periods for this region. We thus conclude that presence methods may better estimate species richness given limited study periods (less than 10 trips), but that for longer or more frequent sampling periods a combination of presence and distance sampling are clearly more effective estimates of overall richness.

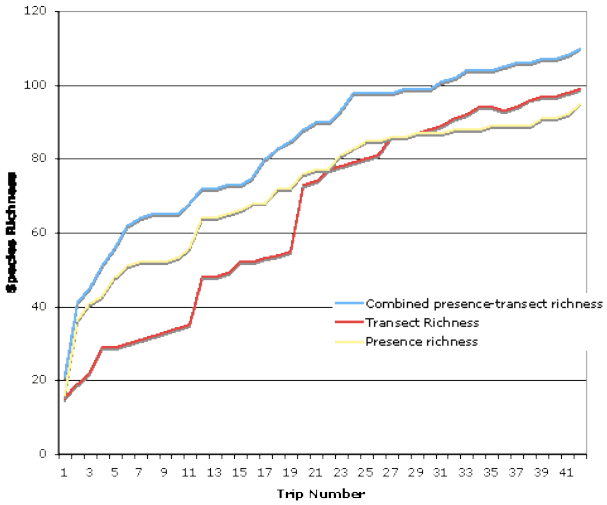



Figure 5–9. A comparison of the accrual of new species over time by method.

## Abundance

There are a number of methods to explore the species abundance data. One of the most traditional is via rank abundance charts (Figures 5–10 and 5–11). These rank abundance charts show the number of registrations per species across the X axis (though sometimes rank-abundance charts show the number of individuals of a given species in a community; Case 1999), with the number of species corresponding to these registrations along the Y axis. Both presence and distance sampling methodologies show similar trends, with many "rare" species (that is, species with only a handful of registrations over the sampling period, concentrated on the lefthand side of the chart) and a relatively small number of common species (concentrated on the righthand side of the chart). The presence data is flatter than the distance sampling data, while the latter approaches something closer to a classic "hollow ball" distribution (Magurran 2003), particularly if the data is binned into clusters of five to 10 registrations per species.

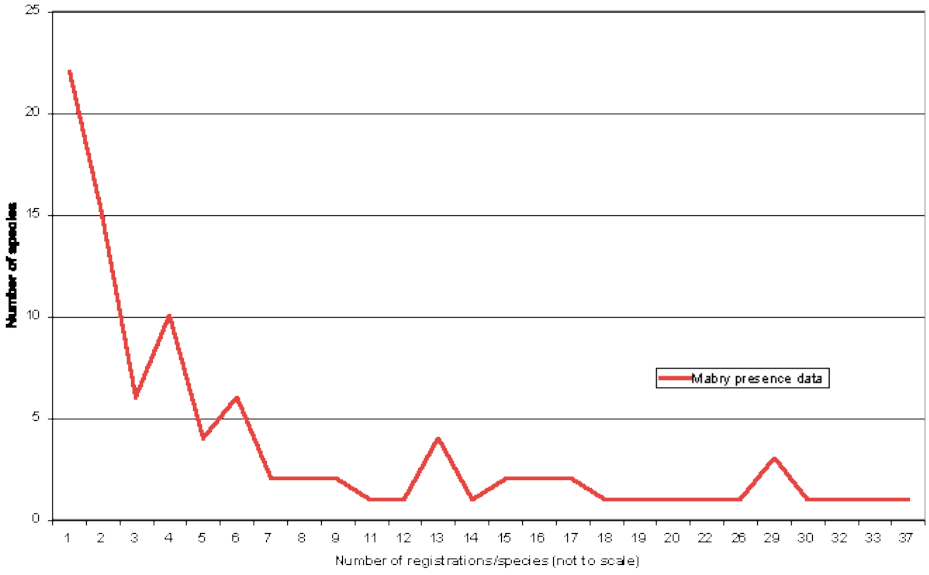



Figure 5–10. The rank abundance of presence registrations at Camp Mabry.

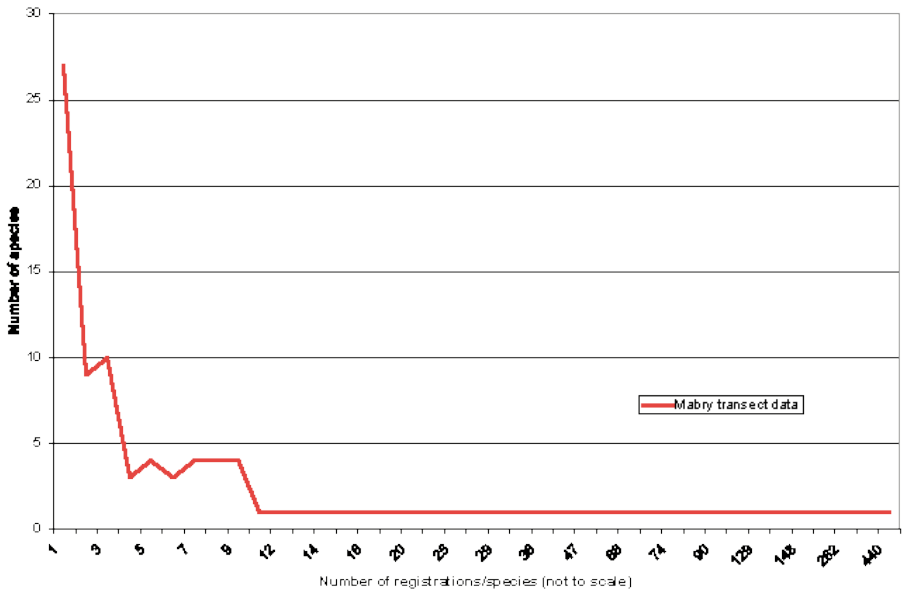



Figure 5–11. Rank abundance of distance sampling registrations at Camp Mabry.

There are a number of reasons for these differences. Perhaps the most basic reflects the fewer maximum number of presence registrations possible (43) for any given species. Northern cardinals (*Cardinalis cardinalis*), for instance, were registered present on 37 of 43 trips. In contrast, the upper limit for registrations using distance sampling is theoretically unlimited. With both methods, the minimum number of registrations is, of course, one. There are far more rare species represented by distance sampling than by presence methods, and the relative distance between common and rare species is much greater. Magurran (2003) and the long heritage of community ecology studies across a wide range of taxa would suggest that the distance sampling data is more typical for many types of communities and thus more accurate (e.g., Case 1999, Ricklefs 2000). Further, the distance sampling data matches our experiences in the field far more closely than the presence data.

In particular, the presence data tends to over represent species that are resident for long periods at Camp Mabry and that are territorial. Thus, we probably observed three Loggerhead shrikes (*Lanius ludovicianus*) over the full study period, including one individual that established a territory along our driving route. We observed this individual on almost half of our trips, but standard presence methodology does not compensate for multiple observations of the same individual. Thus, Loggerhead shrikes are ranked rather high in abundance with presence methods and more appropriately at a low density using distance sampling.

## THE ECOLOGICAL PLACEMENT OF CAMP MABRY: CHARACTERIZING THE COMMUNITY

In terms of bird community, Camp Mabry lies at the conjunction of a number of different physiographic and ecological zones that influence its composition. Camp Mabry lies near the line roughly demarking eastern from western North American species, though eastern species tend to dominate. Given the physiographic areas of Texas defined by Partners in Flight (PIF), Camp Mabry can also be described as lying at the eastern portion of the Edwards Plateau (also known as the Balcones Canyonlands) and near the western edge of the Oaks and Prairies physiographic area. Looking across these two scales, Camp Mabry straddles (or almost straddles) a number of edges, leading to what might seem like a curious mix of species to an easterner or westerner. Both black-crested and tufted titmouses (*Baeolophus atricristatus* and *Baeolophus bicolor*, western and eastern species, respectively) are found at Camp Mabry, while in Hays county — bordering Travis county (containing Camp Mabry) to the west — only Black-crested titmouse are found, and at Camp Swift to the east only Tufted titmouse are observed. For the overwhelming majority of species, however, eastern analogs are more abundant. The eastern yellow-

shafted morph of the Northern flicker (*Colaptes auratus*) is found rather than the western red-shafted morph, and (eastern) Belted kingfishers were only registered rather than more western Ringed kingfishers (*Ceryle torquatus*) or the more south-western Green kingfishers (*Chloroceryle americana*). Numerous other examples could be provided along these lines (comparable floral examples are documented in Damude et al. 2005).

Camp Mabry's biota is also strongly influenced by its presence in an urban environment, which can blur the characteristics of its historic presettlement ecoregion. As with many taxa, urban spaces can tend to offer openings for exotic species and new opportunities for some existing natives. Some of these species could be considered hyperabundant. Our earliest training surveys included counts of White-winged doves (*Zenaida asiatica,* native with a boom in urban populations over the twentieth century), Rock pigeons (*Columba livia,* European in origin), House sparrows (*Passer domesticus,* European in origin), and Great-tailed grackles (*Quiscalus mexicanus,* Central American in origin with a dramatic twentieth-century range expansion), but we found that surveying these species interfered extensively with the registration of other species at lower densities. From a year-round perspective, these four species may constitute 20 percent of the avifauna biomass of Camp Mabry and the greater Austin area though together they only make up 3.3 percent of the total richness we observed.[12] These species were overwhelmingly concentrated in the large unforested areas of Camp Mabry — regions like the parade ground and parking lots with little native vegetation, cover, or forage, and that are viewed as desolate and barren by most other species.

Typical native urban-adapted species are exemplified by Northern cardinal, Blue jay (*Cyanocitta cristata*), Carolina wren (*Thryothorus ludovicianus*), both species of

[12] The highest densities for the birds we observed over the study period were on the order of 4 to 5 birds per hectare (for Northern Cardinals etc.), while our best estimate for the four birds we did not focus on may be as high as 10 to 12 birds per hectare per species.

titmouses, Mourning dove (*Zenaida macroura*), and Northern mockingbird (*Mimus polyglottos)*, all of which are residents, as well as migrants such as Bewick's wren (*Thryomanes bewickii*), White-eyed vireo (*Vireo griseus*), and Ruby-crowned kinglet (*Regulus calendula*). These species seem to be able to tolerate disturbance and a wide range of native and exotic vegetation cover; they are all habitat generalists, at least in an urban setting (Lockwood and Freeman 2004). Indeed, the most common species at Camp Mabry are probably all of such a type.

**Endangered and Threatened Species**

Three major agencies relevant to this study publish large-scale recommendations on species of particular risk of extinction because they have small, localized, or declining populations: the U.S. Fish and Wildlife Service, Texas Parks and Wildlife, and Partners in Flight (PIF). These groups often work with the same bodies of data, though they may analyze and interpret this data in contrasting ways. The first two groups cite the only endangered species that was observed at Camp Mabry: the Golden-cheeked warbler.

PIF is a nongovernmental organization that works very closely with other NGOs and federal, state, and local conservation and wildlife management authorities in evaluating the status of North American avian populations and species. Of these three groups, PIF is the only organization that (a) focuses exclusively on birds and (b) evaluates trends by defined physiographic and conservation regions (Carter et al. 2000).

Species of concern to all three groups are included in Supplementes 6 and 7, tailored for species that are reasonably possible to be found in Travis county. Only Bewick's wren is likely to breed regularly at Camp Mabry, though Scissor-tailed flycatcher (*Tyrannus forficatus*), Painted bunting (*Passerina ciris*), Black-chinned hummingbird (*Archilocus alexandri*), Rufous-crowned sparrow (*Aimophila ruficeps*), and

Cave swallow (*Petrochelidon fulva*) are potential breeders observed. Orchard oriole (*Icterus spurius*), Swainson's hawk *(Buteo swainsoni*), Wood thrush (*Hylocichla mustelina*), and Dickcissel (*Spiza americana*) are observed species that may use Camp Mabry, particularly during migration periods (Elphick et al. 2001, Lockwood 2001).

**Diversity and Abundance Hotspots**

The citation of areas that have higher avian diversity is based strictly on transect data, which is the only geographic means of constraining registrations at Camp Mabry. Transects varied the total number of registrations, which spanned from 212 to 487 registrations. The number of samples per transects ranged between 10 and 12, with a mean of 11 (Table 5–5). Once the number of registrations was normalized for the number of times a transect was run or sampled, several interesting patterns emerge.

| Transect | Total Registrations | Transect Runs | Registrations/Run |
|---|---|---|---|
| **1** | 384 | 11 | 34.9 |
| **2** | 307 | 10 | 30.7 |
| **3** | 368 | 12 | 30.7 |
| **4** | 487 | 12 | 40.6 |
| **5** | 212 | 12 | 17.7 |
| **6** | 472 | 10 | 47.2 |
| **7** | 286 | 11 | 26.0 |
| **8** | 212 | 11 | 19.3 |
| **mean** | 341 | 11.1 | 30.9 |
| | Zone 1 mean | 11.2 | 32.1 |
| | Zone 2 mean | 11.0 | 30.1 |

Table 5–5. Abundance levels of birds by transect at Camp Mabry, Austin, Texas.

The two zones did not different in their abundance means, though the variance did differ substantially, suggesting that the habitat is of higher quality in zone 1. In addition, there was a great deal of variance between transects in relative abundances, notably with transects 4 and 6. Explaining the abundance of transect 6 is relatively easy: there is a great deal of water between two ponds and the creek and visibility is high for visual

registrations. Transect 4 also has little closed canopy space. Moreover, the nearby residential properties may attract additional birds through feeders and a high plant diversity. On the other hand, there is little or no standing water along this transect — indeed, there is more *Opuntia* on this transect than on any other. Moreover, the proximity of transect 4 to the entrance road always ensured a lot of aural disturbance. What seems even odder is the very low abundance seen on transect 5, which lies between 4 and 6. The vegetation zonation on Figure 5–7 suggests that transect 5 is on highly disturbed land, as does the associated Mabry Plant Report. However, this transect is even closer to the entrance road, and the transect itself has great (and sudden) physical relief; it is a challenging transect to sample. Given its strenuous nature, it is possible that this transect had built-in distractions that detracted from the effectiveness of spotters.

Richness also varied by transect (Table 5–6). The two zones did not differ meaningfully in overall species richness, although the transects within each zone show great variance from one another. Again, zone 1 has less variance per transect, which is suggestive of higher quality (and more even) habitat. Transect 6 appears as a hotspot. The burst of species there is substantially explained by the presence of riparian habitat, which attracted species that were either never or only rarely seen on other transects. Transect 3, the next most-rich region, is another transect with riparian habitat (though transect 7, which also runs along a creek, does not appear remarkable for its richness). The other seven transects except 6 are clustered fairly near one another. The lowest richness is on transect 5, and the same factors used to explain its low abundance above probably apply with regard to richness as well.

| Transect | Species Richness | |
|---|---|---|
| **1** | 41 | |
| **2** | 42 | |
| **3** | 51 | |
| **4** | 47 | |
| **5** | 38 | |
| **6** | 65 | |
| **7** | 42 | |
| **8** | 44 | |
| **Total mean** | 46.3 | |
| | Zone 1 mean | 44.7 |
| | Zone 2 mean | 47.2 |

Table 5–6. Species richness of birds by transect at Camp Mabry, Austin, Texas.

### Diversity by Transect

Given the two forms of making registrations, there are a number of ways of looking at the diversity data. Distance sampling is a method that is designed to generate an estimate of the density of a species — so many organisms per unit area. This data has some important constraints, as discussed in more detail above, that particularly concern the number of registrations. As with most sampling processes, more data usually means better analysis. We ranked all species observed by transect with 10 or more registrations (Table 5–7). These rankings were totaled by species and then normalized by the number of transects that included the species, which generated a transformed rank of the most abundant species of Camp Mabry. Actual measured densities are listed in Supplement 8.

| | Transects | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species[13]** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **Summary of Ranks** | **Normalized by # of rankings** | **Transformed Rank** |
| NOCA | 2 | | 1 | 1 | 1 | 1 | 1 | 3 | 10 | 7 | 1.4 |
| CARW | 3 | 1 | 3 | 2 | 3 | 2 | 2 | 1 | 17 | 8 | 2.1 |
| BLJA | 1 | 2 | 2 | 3 | 4 | 4 | 3 | 2 | 21 | 8 | 2.6 |
| CACH | | 4 | 5 | 4 | 2 | 7 | | | 22 | 5 | 4.4 |
| NOMO | | 8 | 4 | 6 | 6 | 5 | 4 | 4 | 37 | 7 | 5.3 |
| HOFI | | 5 | 7 | 10 | | 3 | 6 | 7 | 38 | 6 | 6.3 |
| RCKI | 4 | 3 | 6 | 8 | | 11 | | | 32 | 5 | 6.4 |
| LEGO | | | | 7 | | | | | 7 | 1 | 7.0 |
| AMCR | | 7 | 9 | 11 | 5 | 12 | 5 | 5 | 54 | 7 | 7.7 |
| BARS | | | | | | 8 | | | 8 | 1 | 8.0 |
| WEVI | | | | 9 | 7 | 9 | 7 | | 32 | 4 | 8.0 |
| RBWO | 8 | 6 | 8 | 15 | | 6 | | | 43 | 5 | 8.6 |
| MODO | | | 11 | 5 | | 10 | | | 26 | 3 | 8.7 |
| BCTI | 5 | | | 13 | | | | | 18 | 2 | 9.0 |
| CHSW | 7 | | | 15 | | 13 | | 6 | 41 | 4 | 10.3 |
| BEWR | | | 10 | 12 | | | | | 22 | 2 | 11.0 |
| YRWA | 6 | | | 14 | | 14 | | | 34 | 3 | 11.3 |
| COGR | | | | | | 15 | | | 15 | 1 | 15.0 |

Table 5–7. Density rankings of birds by transect and normalized across transects at Camp Mabry, Austin, Texas.

## Diversity by Time: Critical Periods

Diversity levels made steep climbs during several periods (Figure 5–7). There was an initial climb over the first six trips to Camp Mabry, which corresponded in part to the fall southern migration in September through early November. A large jump also occurred

[13] For purposes of space, the American Ornithological Union four-letter species code is used here. Supplement 1 provides a key of these codes with common and scientific names.

during late January and early February (trips 10 through 13), perhaps as a result of the movement of northern species moving somewhat south to escape the most severe portions of winter to the north of Austin. Another large jump occurred in March and early April (trips 19 through 21), when northern spring migration reaches a high point. This latter period extended into early May at a slower rate.

## RESOURCE MANAGEMENT RECOMMENDATIONS

Given the nature of the data we produced, our recommendations fall neatly into two categories: methodologies for future bird surveys, and management of Camp Mabry property to improve avian abundance and diversity.

### Suggestions for Managing Future Avian Research

Our use of multiple sampling methodologies has implications for the implementation of other avian research projects:

- With limited time (<6 trips) or expertise, presence sampling may be sufficient to estimate richness
- Over longer periods, distance sampling provides more accurate estimates of richness and good estimates of abundance and density, especially if combined with presence methods
- Although distance sampling is most often used for research on small numbers of species and the training and implementation and analytical periods require some

forethought, distance sampling is quite appropriate for large-scale multispecies studies

## DISCUSSION: JOINT CONCLUSIONS FROM RICHNESS AND ABUNDANCE RESEARCH AT CAMPS MABRY AND SWIFT

### Interpreting Rarity as Measured Via Distance Sampling and Presence Methods

Rarity in the context of this study has three different levels. Locally, species may be encountered infrequently because they are either (a) difficult to encounter with the survey methods, (b) at low density in the habitat or region being surveyed, or (c) rare in an absolute sense that the number of individuals in a given population is small, as may be the case with isolated populations, populations passing through some low point of stochastic variability, sink populations, or some endangered and threatened species in serious decline. These three categories are not mutually exclusive. We confirmed an encounter with a Golden-cheeked warbler (*Dendroica chrysoparia*) in March 2004 at Camp Mabry (and suspected that more than one was present based on vocalizations; both were probably males). Two individuals across 145.9 hectares over 14 months of surveys is a very low density. In some areas during particular periods, this species is abundant and easily encountered. At other times, the species is very quiet and difficult to detect though present. In marginal habitats, the numbers of individuals are often small. And throughout the whole of the species's breeding range, populations are in overall decline. We believe it very unlikely that the species has bred (or attempted to breed) at Camp Mabry for many years.

At Camp Swift, Chuck-will's-widow (*Caprimulgus carolinensis*) was found only once during the survey period, a species cited by Partners in Flight as needing particular

attention. How should "rarity" in terms of data collected at both sites be interpreted in light of what else is known about these species? In some areas and during particular periods, both species are abundant and easily encountered. Moreover, Chuck-will's-widow is most detectable aurally, and almost all vocalization occurs at night. At other times, the species is very quiet and difficult to detect though present. While overall numbers are in decline, we believe that Chuck-will's-widow may have a large and healthy population at Camp Swift, with local breeding. The reason we believe this is that we only conducted one night survey at Camp Swift (15 August 2004), during which we heard numerous individuals vocalizing. However, because we could not run transects in the dark, we sampled only using presence methods, and thus we cannot quantify the population using the same systematic method used for diurnal species.

Thus, these limited registrations are not very informative in helping us to decide between several very divergent hypotheses:

- Chuck-will's-widows and Golden-cheeked warblers only pass through both properties on their way to better-quality habitat.
- These properties are within the range of each species and represents a large enough area of habitat to support a breeding population.

If the latter case is true, we cannot further infer that the population is stable, increasing, or decreasing by relying on data from a single year. A real danger exists in interpreting a low frequency of registrations as the equivalent of declining population size or absolute rarity throughout a region. However, these determinations are difficult to make. A more reasonable conclusion may be that rare species' population status (that is,

the abundance of species who were encountered infrequently) should be evaluated on a case by case basis, and some species may require additional research in order to choose between alternate perspectives on their population health.

**Comparisons between Presence and Distance Sampling**

Accurate diversity estimates are essential to making effective decisions when allocating scarce institutional resources. The data from this research suggests that presence and distance sampling methods differ in how and when they should be applied as diagnostic tools. For instance, at Camp Mabry the two methods differ in how they accrued new species (Figure 5–9). Presence observations resulted in a fairly steep addition of species before leveling off somewhat, reaching the midpoint of the final richness by trip 12, which was the 28th percentile of the total of 43 trips. Distance sampling accrued species more evenly over the study period and reached its richness midpoint by trip 21, though notable jumps occurred during the peak fall and spring migration periods for this region. We thus conclude that presence methods may better estimate species richness given limited study periods (less than 10 trips, especially if these trips were spaced over longer temporal periods than during our study), but that for longer or more frequent sampling periods a combination of presence and distance sampling are clearly more effective estimates of overall richness.

Estimates of abundance, however, showed that the types of species detected different significantly between methods. Distance sampling was most effective at providing reliable and accurate measures of abundance, especially given that both methods used repeated visits to the same localities. Presence methods were not accurate at distinguishing between rare and common species.

## LITERATURE CITED


Bibby, C.J., M. Jones, and S. Marsden. 1998. *Expedition field techniques: bird surveys*. London, UK: Royal Geographical Society.

Bibby, C.J., N.D. Burgess, D.A. Hill, and S. Mustoe. 2000. *Bird census techniques*. Second edition. San Diego, CA: Academic Press.

Buckland, S.T. Submitted. Point transect surveys for songbirds: robust methodologies.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2004. *Advanced distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Carter, M.F., W.C. Hunter, D.N. Pashley, and K.V. Rosenberg. 2000. Setting conservation priorities for landbirds in the United States: The Partners In Flight approach. *Auk* 117:541-548.

Case, T. 1999. *An illustrated guide to theoretical ecology*. Oxford, UK: Oxford University Press.

Jimenez, I., G.A. Londono, C.D. Cadena. 2003. Efficiency, bias, and consistency of visual and aural surveys of curassows (Cracidae) in tropical forests *J. Field Ornithol.*. 74, 210–216.

Lockwood, M.W. 2001. *Birds of the Texas Hill Country*. Austin, Texas: University of Texas Press.

Lockwood, M.W., and B. Freeman. *The TOS handbook of Texas birds*. College Station, TX: Texas A&M Press.

Magurran, A. 2003. *Measuring biological diversity*. Boston, MA: Blackwell Publishers.

Norvell, R.E., F.P. Howe, and J.R. Parrish. 2003. A seven-year comparison of relative-abundance and distance-sampling methods. *The Auk* (120(4): 1013–28.

Palka, D.L. 1996. Effects of Beaufort sea state on the sightability of harbor porpoises in the Gulf of Maine. *Reports of the International Whaling Commission* 46:575-582.

Ricklefs, R.E. 2000. *The economy of nature*. Fifth edition. New York: W.H. Freeman.

Sagarin, R., and F. Michelli. 2001. Climate change in nontraditional datasets. *Science* 294, 811.

Stake, M.M., J. Faaborg, and F.R. Thompson. 2004. The video identification of predators at golden-cheeked warbler nests. *Journal of Field Ornithology* 75(4): 337–344.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/

Supplement 1

**Inventory of Bird Species Observed at Camp Swift, Austin, Texas**

**15 October 2003–18 October 2004**

| **Common Name** | **Four-letter Code** | **Scientific Name** |
|---|---|---|
| Acadian Flycatcher | ACFL | *Empidonax virescens* |
| American Crow | AMCR | *Corvus brachyrhynchos* |
| American Goldfinch | AMGO | *Carduelis tristis* |
| American Kestrel | AMKE | *Falco sparverius* |
| American Robin | AMRO | *Turdus migratorius* |
| American Wigeon | AMWI | *Anas americana* |
| Baltimore Oriole | BAOR | *Icterus galbula* |
| Barn Swallow | BARS | *Hirundo rustica* |
| Bewick's Wren | BEWR | *Thryomanes bewickii* |
| Black Vulture | BLVU | *Coragyps atratus* |
| Black-and-white Warbler | BAWW | *Mniotilta varia* |
| Black-billed Cuckoo | BBCU | *Coccyzus erythropthalmus* |
| Black-crested Titmouse | BCTI | *Baeolophus atricristatus* |
| Black-throated Green Warbler | BTNW | *Dendroica virens* |
| Blue Jay | BLJA | *Cyanocitta cristata* |
| Blue-gray Gnatcatcher | BGGN | *Polioptila caerulea* |
| Broad-winged Hawk | BWHA | *Buteo platypterus* |
| Brown Thrasher | BRTH | *Toxostoma rufum* |
| Brown-headed Cowbird | BHCO | *Molothrus ater* |
| Carolina Chickadee | CACH | *Poecile carolinensis* |
| Carolina Wren | CARW | *Thryothorus ludovicianus* |
| Cattle Egret | CAEG | *Bubulcus ibis* |
| Cave Swallow | CASW | *Petrochelidon fulva* |
| Cedar Waxwing | CEDW | *Bombycilla cedrorum* |
| Cerulean Warbler | CERW | *Dendroica cerulea* |
| Chimney Swift | CHSW | *Chaetura pelagica* |
| Chipping Sparrow | CHSP | *Spizella passerina* |
| Cliff Swallow | CLSW | *Petrochelidon pyrrhonota* |

| | | |
|---|---|---|
| Common Grackle | COGR | *Quiscalus quiscula* |
| Common Ground-Dove | COGD | *Columbina passerina* |
| Cooper's Hawk | COHA | *Accipiter cooperii* |
| Crested Caracara | CRCA | *Caracara cheriway* |
| Dark-eyed Junco | DEJU | *Junco hyemalis* |
| Dickcissel | DICK | *Spiza americana* |
| Double-crested Cormorant | DCCO | *Phalacrocorax auritus* |
| Downy Woodpecker | DOWO | *Picoides pubescens* |
| Eastern Bluebird | EABL | *Sialia sialis* |
| Eastern Kingbird | EAKI | *Tyrannus tyrannus* |
| Eastern Meadowlark | EAME | *Sturnella magna* |
| Eastern Phoebe | EAPH | *Sayornis phoebe* |
| Eastern Towhee | EATO | *Pipilo erythrophthalmus* |
| Eastern Wood-Pewee | EAWP | *Contopus virens* |
| Field Sparrow | FISP | *Spizella pusilla* |
| Fox Sparrow | FOSP | *Passerella iliaca* |
| Franklin's Gull | FRGU | *Larus pipixcan* |
| Gray Catbird | GRCA | *Dumetella carolinensis* |
| Great Blue Heron | GBHE | *Ardea herodias* |
| Great Crested Flycatcher | GCFL | *Myiarchus crinitus* |
| Great Egret | GREG | *Ardea alba* |
| Great Horned Owl | GHOW | *Bubo virginianus* |
| Greater Roadrunner | GRRO | *Geococcyx californianus* |
| Great-tailed Grackle | GTGR | *Quiscalus mexicanus* |
| Green Heron | GRHE | *Butorides virescens* |
| Hairy Woodpecker | HAWO | *Picoides villosus* |
| Harris's Sparrow | HASP | *Zonotrichia querula* |
| Hermit Thrush | HETH | *Catharus guttatus* |
| House Finch | HOFI | *Carpodacus mexicanus* |
| House Wren | HOWR | *Troglodytes aedon* |
| Indigo Bunting | INBU | *Passerina cyanea* |
| Killdeer | KILL | *Charadrius vociferus* |
| Ladder-backed Woodpecker | LBWO | *Picoides scalaris* |
| Lesser Goldfinch | LEGO | *Carduelis psaltria* |
| Lincoln's Sparrow | LISP | *Melospiza lincolnii* |
| Loggerhead Shrike | LOSH | *Lanius ludovicianus* |
| Long-billed Curlew | LBCU | *Numenius americanus* |
| Mississippi Kite | MIKI | *Ictinia mississippiensis* |
| Mourning Dove | MODO | *Zenaida macroura* |
| Nashville Warbler | NAWA | *Vermivora ruficapilla* |
| Northern Cardinal | NOCA | *Cardinalis cardinalis* |

| | | |
|---|---|---|
| Northern Flicker | NOFL | *Colaptes auratus* |
| Northern Harrier | NOHA | *Circus cyaneus* |
| Northern Mockingbird | NOMO | *Mimus polyglottos* |
| Northern Parula | NOPA | *Parula americana* |
| Northern Rough-winged Swallow | NRWS | *Stelgidopteryx serripennis* |
| Orange-crowned Warbler | OCWA | *Vermivora celata* |
| Painted Bunting | PABU | *Passerina ciris* |
| Pileated Woodpecker | PIWO | *Dryocopus pileatus* |
| Pine Warbler | PIWA | *Dendroica pinus* |
| Purple Martin | PUMA | *Progne subis* |
| Pyrrhuloxia | PYRR | *Cardinalis sinuatus* |
| Red-bellied Woodpecker | RBWO | *Melanerpes carolinus* |
| Red-eyed Vireo | REVI | *Vireo olivaceus* |
| Red-shouldered Hawk | RSHA | *Buteo lineatus* |
| Red-tailed Hawk | RTHA | *Buteo jamaicensis* |
| Red-winged Blackbird | RWBL | *Agelaius phoeniceus* |
| Ruby-crowned Kinglet | RCKI | *Regulus calendula* |
| Ruby-throated Hummingbird | RTHU | *Archilochus colubris* |
| Sandhill Crane | SACR | *Grus canadensis* |
| Savannah Sparrow | SAVS | *Passerculus sandwichensis* |
| Scissor-tailed Flycatcher | STFL | *Tyrannus forficatus* |
| Sharp-shinned Hawk | SSHA | *Accipiter striatus* |
| Snowy Egret | SNEG | *Egretta thula* |
| Song Sparrow | SOSP | *Melospiza melodia* |
| Spotted Towhee | SPTO | *Pipilo maculatus* |
| Summer Tanager | SUTA | *Piranga rubra* |
| Swainson's Thrush | SWTH | *Catharus ustulatus* |
| Tufted Titmouse | TUTI | *Baeolophus bicolor* |
| Turkey Vulture | TUVU | *Cathartes aura* |
| Upland Sandpiper | UPSA | *Bartramia longicauda* |
| Vesper Sparrow | VESP | *Pooecetes gramineus* |
| White-crowned Sparrow | WCSP | *Zonotrichia leucophrys* |
| White-eyed Vireo | WEVI | *Vireo griseus* |
| White-throated Sparrow | WTSP | *Zonotrichia albicollis* |
| Winter Wren | WIWR | *Troglodytes troglodytes* |
| Wood Duck | WODU | *Aix sponsa* |
| Yellow-bellied Sapsucker | YBSA | *Sphyrapicus varius* |
| Yellow-billed Cuckoo | YBCU | *Coccyzus americanus* |
| Yellow-breasted Chat | YBCH | *Icteria virens* |

| | | |
|---|---|---|
| Yellow-rumped Warbler | YRWA | *Dendroica coronata* |
| Yellow-shafted Flicker | YSFL | *Colaptes a. auratus* |
| Yellow-throated Warbler | YTWA | *Dendroica dominica* |

**SUPPLEMENT 2**

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**SUPPLEMENT 3**

**Partners in Flight Species of Concern**

**PIF Code Key**

| PIF Code | Explanation |
|---|---|
| I.A. | Extremely high priority |
| I.B. | High priority |
| II.A. | High regional concern |
| II.B. | High regional responsibility |
| II.C. | High regional threats |
| III. | Moderate overall priority |

**Overwintering species of concern**

| Common name | Scientific name | PIF code | Observed at Camp Swift? | Likely at Camp Swift? |
|---|---|---|---|---|
| Horned Grebe | *Podiceps auritus* | II.A. | Yes | Migrant |
| American Wigeon | *Anas Americana* | II.A. | Yes | Migrant |
| Northern Pintail | *Anas acuta* | II.A. | No | Migrant |
| Canvasback | *Aythya valisineria* | II.A. | No | Migrant |
| Redhead | *Aythya Americana* | II.C. | No | Migrant |
| Northern Harrier | *Circus cyaneus* | II.A. | Yes | Yes |
| Northern Bobwhite | *Colinus virginianus* | I. | No | Yes |
| Killdeer | *Charadrius vociferous* | II.A. | Yes | Yes |
| Long-billed Curlew | *Numenius americanus* | I. | yes | Migrant |
| American Woodcock | *Scolopax minor* | I. | Yes | Yes |
| Short-eared Owl | *Asio flammeus* | II.C. | No | Uncertain |
| Red-headed Woodpecker | *Melanerpes erythrocephalus* | I. | No | No |
| Yellow-bellied Sapsucker | *Sphyrapicus varius* | II.A. | Yes | Yes |
| Red-cockaded Woodpecker | *Picoides borealis* | I. | No | No |
| Loggerhead Shrike | *Lanius ludovicianus* | I. | Yes | Yes |

| | | | | |
|---|---|---|---|---|
| Carolina Chickadee | *Poecile carolinensis* | II.A. | Yes | Yes |
| Brown Creeper | *Certhia Americana* | II.A. | No | Yes |
| Bewick's Wren | *Thryomanes bewickii* | II.C. | Yes | Yes |
| Sedge Wren | *Cistothorus platensis* | II.C. | No | No |
| Brown Thrasher | *Toxostoma rufum* | II.A. | Yes | Yes |
| Sprague's Pipit | *Anthus spragueii* | I. | No | Yes |
| Spotted Towhee | *Pipilo maculates* | II.A. | Yes | Yes |
| Eastern Towhee | *Pipilo erythrophthalmus* | II.A. | Yes | Yes |
| Field Sparrow | *Spizella pusilla* | I. | Yes | Yes |
| Vesper Sparrow | *Pooecetes gramineus* | II.A. | Yes | Yes |
| Lark Sparrow | *Chondestes grammacus* | II.A. | Yes | Yes |
| Lark Bunting | *Calamospiza melanocorys* | II.C. | No | Yes |
| Henslow's Sparrow | *Ammodramus henslowii* | I. | No | Yes |
| Grasshopper Sparrow | *Ammodramus savannarum* | II.A. | Yes | Yes |
| Le Conte's Sparrow | *Ammodramus leconteii* | I. | No | Yes |
| Harris's Sparrow | *Zonotrichia querula* | I. | Yes | Yes |
| McCown's Longspur | *Calcarius mccownii* | I. | No | Yes |
| Smith's Longspur | *Calcarius pictus* | I. | No | Yes |
| Chestnut-collared Longspur | *Calcarius ornatus* | I. | No | Yes |
| Eastern Meadowlark | *Sturnella magna* | II.A. | Yes | Yes |
| Rusty Blackbird | *Euphagus carolinus* | II.A. | No | Yes |

**PIF Oaks and Prairies Breeding Species of Concern**

| Common name | Scientific name | PIF code | Observed at Camp Swift? | Likely at Camp Swift? |
|---|---|---|---|---|
| Reddish Egret | *Egretta rufescens* | I. | No | No |
| Cattle Egret | *Bubulcus ibis* | III | Yes | Yes |
| Green Heron | *Butorides virescens* | II.A. | Yes | Yes |
| Black Vulture | *Coragyps atratus* | III | Yes | Yes |
| Turkey Vulture | *Cathartes aura* | III | Yes | Yes |
| Swallow-tailed Kite | *Elanoides forficatus* | I. | No | No |
| Crested Caracara | *Caracara cheriway* | III | Yes | Yes |
| Greater Prairie- | *Tympanuchus* | I. | No | No |

| | | | | |
|---|---|---|---|---|
| Chicken | *cupido* | | | |
| Northern Bobwhite | *Colinus virginianus* | II.A. | Yes | Yes |
| Black Rail | *Laterallus jamaicensis* | I. | No | No |
| Killdeer | *Charadrius vociferous* | II.A. | Yes | Yes |
| American Oystercatcher | *Haematopus palliates* | I. | No | No |
| American Avocet | *Recurvirostra Americana* | II.C. | No | No |
| American Woodcock | *Scolopax minor* | III | Yes | Yes |
| Sandwich Tern | *Sterna sandvicensis* | II.A. | No | No |
| Inca Dove | *Columbina inca* | II.B. | Yes (MAPS) | Yes |
| Common Ground-Dove | *Columbina passerina* | III | Yes | Yes |
| Yellow-billed Cuckoo | *Coccyzus americanus* | I. | Yes | Yes |
| Burrowing Owl | *Athene cunicularia* | II.C. | No | Uncertain |
| Chuck-will's-widow | *Caprimulgus carolinensis* | I. | Yes | Yes |
| Chimney Swift | *Chaetura pelagica* | II.A. | Yes | Yes |
| Black-chinned Hummingbird | *Archilocus alexandri* | I. | Yes (MAPS) | Yes |
| Red-headed Woodpecker | *Melanerpes erythrocephalus* | III | No | Yes |
| Great Crested Flycatcher | *Myiarchus crinitus* | II.A. | Yes | Yes |
| Scissor-tailed Flycatcher | *Tyrannus forficatus* | I. | Yes | Yes |
| Loggerhead Shrike | *Lanius ludovicianus* | II.A. | Yes | Yes |
| Carolina Chickadee | *Poecile carolinensis* | II.A. | Yes | Yes |
| Marsh Wren | *Cistothorus palustris* | II.C. | No | No |
| Wood Thrush | *Hylocichla mustelina* | II.C. | Yes (MAPS) | Yes |
| Northern Mockingbird | *Mimus polyglottos* | III | Yes | Yes |
| Prairie Warbler | *Dendroica discolor* | III | No | Yes |
| Prothonotary Warbler | *Protonotaria citrea* | I. | No | Migrant |
| Worm-eating Warbler | *Helmitheros vermivorum* | I. | No | Yes |
| Swainson's | *Limnothlypis* | I. | Yes (MAPS) | Yes |

| | | | | |
|---|---|---|---|---|
| Warbler | *swainsonii* | | | |
| Louisiana Waterthrush | *Seiurus motacilla* | II.C. | No | Possible |
| Kentucky Warbler | *Oporornis formosus* | I. | Yes | Yes |
| Lark Sparrow | *Chondestes grammacus* | II.A. | Yes | Yes |
| Northern Cardinal | *Cardinalis cardinalis* | III | Yes | Yes |
| Painted Bunting | *Passerina ciris* | I. | Yes | Yes |
| Dickcissel | *Spiza Americana* | II.C. | Yes | Yes |
| Eastern Meadowlark | *Sturnella magna* | II.A. | Yes | Yes |
| Great-tailed Grackle | *Quiscalus mexicanus* | III | Yes | Yes |

**SUPPLEMENT 4**

## Distance 4.1 raw data for all species observed at Camp Swift with 10 or more registrations

Key to abbreviations
Status: 1 – ran with no constrained variables, 2 – ran with some constraints
Name: 4-letter species abbreviation, or all (for all bird species)
Delta AIC: minimum AIC, calculated within survey and data filter
AIC: Akaike Information Criterion value
ESW: Effective strip width
D: Density of individuals (per hectares)
D LCL: Density of individuals analytic lower confidence limit
D UCL: Density of individuals analytic upper confidence limit
D CV: Density of individuals analytic coefficient of variation

### Comparison of transects and whole-Swift data: all species

| Status | Name | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|
| 2 | All data | 0 | 11971.62 | 23.2938 | 3.12 | 2.53 | 3.84 | 0.1060 |
| 1 | 1 | 0 | 2312.78 | 107.2230 | 1.98 | 1.16 | 3.36 | 0.2064 |
| 1 | 2 | 0 | 1328.58 | 80.3935 | 1.33 | 0.89 | 1.99 | 0.1708 |
| 2 | 3 | 0 | 643.07 | 41.3213 | 1.01 | 0.46 | 2.19 | 0.3700 |
| 1 | 4 | 0 | 1281.91 | 36.3264 | 2.53 | 1.66 | 3.86 | 0.2064 |
| 1 | 5 | 0 | 499.40 | 23.8411 | 4.40 | 2.06 | 9.41 | 0.2819 |
| 1 | 6 | 0 | 856.72 | 21.1860 | 3.93 | 2.63 | 5.89 | 0.2010 |
| 1 | 7 | 0 | 609.68 | 15.5128 | 6.04 | 3.55 | 10.30 | 0.2725 |
| 1 | 8 | 0 | 1183.53 | 44.2480 | 2.41 | 1.48 | 3.92 | 0.2385 |
| 1 | 9 | 0 | 1052.21 | 23.6722 | 3.71 | 2.45 | 5.62 | 0.2119 |
| 1 | 10 | 0 | 402.41 | 57.1802 | 1.05 | 0.35 | 3.13 | 0.4442 |
| 1 | 11 | 0 | 768.41 | 47.0266 | 1.31 | 0.74 | 2.31 | 0.2579 |
| 1 | 12 | 0 | 1625.90 | 78.0773 | 1.12 | 0.66 | 1.90 | 0.2491 |
| 2 | 13 | 0 | 1467.22 | 53.9621 | 1.87 | 1.17 | 2.98 | 0.2078 |
| 2 | 14 | 0 | 973.92 | 58.0049 | 1.48 | 0.79 | 2.79 | 0.3028 |
| 2 | 15 | 0 | 1161.66 | 31.5578 | 3.10 | 1.08 | 8.88 | 0.5707 |
| 1 | 16 | 0 | 1820.86 | 83.5105 | 1.74 | 1.27 | 2.37 | 0.1554 |

### Comparison of all-Swift data for all species with >9 registrations

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 2 | ALL SWIFT | 2 | 0 | 11971.62 | 23.294 | 3.1189 | 2.5345 | 3.8380 | 0.1060 |
| 1 | NOCA | 1 | 0 | 1583.60 | 26.323 | 0.3856 | 0.2994 | 0.4965 | 0.1290 |
| 1 | CARW | 1 | 0 | 1851.03 | 40.764 | 0.2600 | 0.2093 | 0.3231 | 0.1106 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | BGGN | 1 | 0 | 401.96 | 15.843 | 0.1894 | 0.1010 | 0.3549 | 0.3260 |
| 1 | WEVI | 1 | 0 | 1018.76 | 38.136 | 0.1573 | 0.1114 | 0.2222 | 0.1764 |
| 1 | YRWA | 1 | 0 | 128.07 | 8.345 | 0.1198 | 0.0441 | 0.3259 | 0.5308 |
| 1 | CACH | 1 | 0 | 670.09 | 34.385 | 0.1192 | 0.0812 | 0.1752 | 0.1967 |
| 1 | AMCR | 2 | 0 | 3720.11 | 170.035 | 0.0938 | 0.0776 | 0.1134 | 0.0966 |
| 1 | RCKI | 1 | 0 | 314.65 | 25.325 | 0.0849 | 0.0519 | 0.1388 | 0.2521 |
| 2 | TUTI | 2 | 0 | 544.86 | 37.042 | 0.0810 | 0.0531 | 0.1235 | 0.2159 |
| 1 | PABU | 1 | 0 | 478.22 | 43.742 | 0.0629 | 0.0351 | 0.1127 | 0.3017 |
| 2 | FISP | 2 | 0 | 248.55 | 29.240 | 0.0513 | 0.0222 | 0.1183 | 0.4416 |
| 1 | DICK | 1 | 0 | 363.87 | 44.087 | 0.0488 | 0.0263 | 0.0904 | 0.3193 |
| 1 | MODO | 1 | 0 | 560.04 | 73.118 | 0.0410 | 0.0277 | 0.0609 | 0.2017 |
| 2 | SAVS | 1 | 0 | 47.38 | 9.346 | 0.0374 | 0.0104 | 0.1354 | 0.6803 |
| 2 | AMRO | 2 | 0 | 234.07 | 35.251 | 0.0369 | 0.0171 | 0.0794 | 0.4018 |
| 1 | BHCO | 1 | 0 | 289.37 | 49.104 | 0.0336 | 0.0186 | 0.0608 | 0.3061 |
| 1 | WTSP | 1 | 0 | 265.41 | 47.945 | 0.0323 | 0.0153 | 0.0685 | 0.3933 |
| 1 | RBWO | 1 | 0 | 817.88 | 129.708 | 0.0301 | 0.0217 | 0.0417 | 0.1664 |
| 1 | NOMO | 1 | 0 | 245.44 | 50.300 | 0.0268 | 0.0148 | 0.0485 | 0.3055 |
| 1 | YBCU | 1 | 0 | 187.72 | 44.447 | 0.0236 | 0.0117 | 0.0475 | 0.3635 |
| 1 | CHSP | 1 | 0 | 76.99 | 28.388 | 0.0176 | 0.0074 | 0.0421 | 0.4613 |
| 2 | DOWO | 1 | 0 | 253.98 | 86.560 | 0.0156 | 0.0088 | 0.0275 | 0.2912 |
| 1 | SUTA | 1 | 0 | 202.71 | 68.894 | 0.0152 | 0.0083 | 0.0281 | 0.3165 |
| 2 | TUVU | 2 | 0 | 314.27 | 106.774 | 0.0136 | 0.0075 | 0.0247 | 0.3088 |
| 2 | SOSP | 1 | 0 | 65.56 | 29.607 | 0.0135 | 0.0040 | 0.0460 | 0.6717 |
| 2 | EAPH | 2 | 0 | 103.49 | 48.918 | 0.0112 | 0.0047 | 0.0270 | 0.4509 |
| 2 | SPTO | 1 | 0 | 108.06 | 59.081 | 0.0110 | 0.0051 | 0.0238 | 0.4035 |
| 2 | BARS | 1 | 0 | 68.97 | 41.275 | 0.0109 | 0.0032 | 0.0376 | 0.6609 |
| 1 | BLJA | 1 | 0 | 484.35 | 195.210 | 0.0108 | 0.0065 | 0.0177 | 0.2552 |
| 1 | PIWO | 1 | 0 | 604.57 | 272.185 | 0.0092 | 0.0063 | 0.0133 | 0.1904 |
| 2 | RTHU | 2 | 0 | 76.07 | 44.053 | 0.0091 | 0.0027 | 0.0305 | 0.6317 |
| 2 | CLSW | 1 | 0 | 63.18 | 45.768 | 0.0087 | 0.0023 | 0.0330 | 0.7161 |
| 1 | RSHA | 1 | 0 | 589.76 | 277.408 | 0.0087 | 0.0063 | 0.0119 | 0.1628 |
| 2 | PIWA | 1 | 0 | 138.25 | 90.221 | 0.0078 | 0.0037 | 0.0164 | 0.3910 |
| 2 | PUMA | 1 | 0 | 29.72 | 31.955 | 0.0063 | 0.0011 | 0.0370 | 0.8582 |
| 2 | LISP | 1 | 0 | 38.89 | 39.993 | 0.0063 | 0.0013 | 0.0304 | 0.8230 |
| 1 | EAME | 1 | 0 | 157.98 | 120.255 | 0.0062 | 0.0026 | 0.0152 | 0.4725 |
| 2 | VESP | 1 | 0 | 41.91 | 41.119 | 0.0061 | 0.0014 | 0.0273 | 0.8149 |
| 1 | BCTI | 1 | 0 | 123.19 | 100.283 | 0.0060 | 0.0023 | 0.0155 | 0.5075 |
| 1 | NOFL | 1 | 0 | 163.34 | 133.953 | 0.0056 | 0.0027 | 0.0118 | 0.3890 |
| 2 | BAOR | 1 | 0 | 82.59 | 87.991 | 0.0051 | 0.0009 | 0.0278 | 1.0377 |
| 2 | RWBL | 1 | 0 | 87.12 | 92.377 | 0.0049 | 0.0016 | 0.0148 | 0.6051 |
| 1 | UPSA | 1 | 0 | 101.07 | 105.379 | 0.0047 | 0.0020 | 0.0110 | 0.4401 |
| 1 | INBU | 1 | 0 | 143.16 | 157.206 | 0.0041 | 0.0018 | 0.0095 | 0.4383 |
| 1 | AMKE | 1 | 0 | 117.69 | 148.583 | 0.0037 | 0.0016 | 0.0085 | 0.4385 |
| 1 | REVI | 1 | 0 | 198.92 | 234.577 | 0.0036 | 0.0017 | 0.0078 | 0.4024 |
| 2 | CAEG | 1 | 0 | 95.47 | 175.324 | 0.0026 | 0.0008 | 0.0084 | 0.6424 |
| 2 | CASW | 1 | 0 | 16.76 | 39.994 | 0.0025 | 0.0001 | 0.0665 | 1.1561 |
| 2 | CEDW | 1 | 0 | 27.04 | 64.943 | 0.0023 | 0.0005 | 0.0112 | 0.8811 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 2 | RTHA | 1 | 0 | 153.86 | 343.965 | 0.0019 | 0.0009 | 0.0042 | 0.4068 |
| 2 | GBHE | 1 | 0 | 81.37 | 227.051 | 0.0015 | 0.0006 | 0.0038 | 0.4675 |
| 2 | SNEG | 1 | 0 | 54.87 | 169.631 | 0.0015 | 0.0005 | 0.0042 | 0.5490 |
| 2 | DCCO | 1 | 0 | 20.42 | 99.985 | 0.0010 | 0.0002 | 0.0050 | 0.8392 |

**Transect 1**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1_ALL | 2 | 0 | 2312.78 | 107.223 | 1.9772 | 1.1638 | 3.3592 | 0.2064 |
| 1 | 1_NOCA | 1 | 0 | 319.22 | 75.486 | 0.4372 | 0.2291 | 0.8343 | 0.2635 |
| 1 | 1_SOSP | 1 | 0 | 86.36 | 45.324 | 0.2206 | 0.0342 | 1.4221 | 0.8007 |
| 1 | 1_PABU | 1 | 0 | 157.14 | 84.473 | 0.1894 | 0.0447 | 0.8025 | 0.5937 |
| 2 | 1_FISP | 1 | 0 | 64.35 | 49.235 | 0.1625 | 0.0227 | 1.1628 | 0.9358 |
| 1 | 1_AMCR | 1 | 0 | 345.33 | 193.320 | 0.1552 | 0.0714 | 0.3373 | 0.3195 |
| 2 | 1_WTSP | 1 | 0 | 106.80 | 78.777 | 0.1523 | 0.0267 | 0.8691 | 0.8014 |
| 2 | 1_NOMO | 2 | 0 | 154.13 | 107.733 | 0.1300 | 0.0312 | 0.5406 | 0.6113 |
| 2 | 1_EAME | 2 | 0 | 67.84 | 54.293 | 0.1289 | 0.0186 | 0.8949 | 0.9317 |
| 1 | 1_CARW | 1 | 0 | 128.16 | 104.000 | 0.1250 | 0.0526 | 0.2969 | 0.4001 |
| 2 | 1_BHCO | 1 | 0 | 47.43 | 93.969 | 0.0532 | 0.0085 | 0.3348 | 0.8643 |
| 2 | 1_CAEG | 1 | 0 | 68.05 | 204.392 | 0.0294 | 0.0031 | 0.2764 | 1.0483 |

**Transect 2**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2_ALL | 2 | 0 | 1328.58 | 80.394 | 1.3268 | 0.8864 | 1.9860 | 0.1708 |
| 2 | 2_YRWA | 1 | 0 | 53.98 | 12.992 | 0.5773 | 0.0694 | 4.8028 | 1.0257 |
| 2 | 2_SAVS | 2 | 0 | 61.85 | 18.931 | 0.3522 | 0.0918 | 1.3515 | 0.6542 |
| 2 | 2_CACH | 2 | 0 | 105.31 | 34.543 | 0.2895 | 0.1085 | 0.7725 | 0.4797 |
| 2 | 2_CARW | 2 | 0 | 219.65 | 67.536 | 0.2715 | 0.1284 | 0.5738 | 0.3589 |
| 1 | 2_NOCA | 1 | 0 | 97.79 | 41.252 | 0.2424 | 0.0872 | 0.6739 | 0.5107 |
| 2 | 2_CASW | 2 | 0 | 82.12 | 39.880 | 0.1881 | 0.0557 | 0.6355 | 0.5848 |
| 1 | 2_PABU | 1 | 0 | 143.02 | 79.228 | 0.1578 | 0.0406 | 0.6124 | 0.6044 |
| 2 | 2_AMCR | 2 | 0 | 256.34 | 125.065 | 0.1533 | 0.0538 | 0.4368 | 0.4537 |
| 2 | 2_FISP | 2 | 0 | 64.96 | 41.824 | 0.1395 | 0.0170 | 1.1477 | 1.1132 |

**Transect 3**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 3_ALL | 1 | 0 | 643.07 | 41.321 | 1.0084 | 0.4636 | 2.1934 | 0.3700 |
| 2 | 3_RCKI | 2 | 0 | 89.69 | 18.265 | 0.3650 | 0.0988 | 1.3478 | 0.6460 |
| 2 | 3_NOCA | 1 | 0 | 174.98 | 42.130 | 0.2901 | 0.1292 | 0.6513 | 0.3915 |
| 2 | 3_BGGN | 2 | 0 | 100.00 | 33.428 | 0.1994 | 0.0362 | 1.0990 | 0.9216 |
| 1 | 3_CARW | 1 | 0 | 228.82 | 70.677 | 0.1887 | 0.1023 | 0.3480 | 0.2867 |
| 1 | 3_CACH | 1 | 0 | 105.72 | 65.665 | 0.0931 | 0.0404 | 0.2145 | 0.3977 |

**Transect 4**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 4_ALL | 2 | 0 | 1281.91 | 36.326 | 2.5292 | 1.6585 | 3.8570 | 0.2064 |
| 1 | 4_BGGN | 1 | 0 | 212.25 | 45.111 | 0.3741 | 0.1056 | 1.3258 | 0.5999 |
| 1 | 4_NOCA | 1 | 0 | 250.34 | 55.434 | 0.3157 | 0.1710 | 0.5828 | 0.2834 |
| 2 | 4_YRWA | 1 | 0 | 60.63 | 25.978 | 0.2165 | 0.0597 | 0.7853 | 0.6324 |
| 2 | 4_RCKI | 2 | 0 | 97.15 | 35.951 | 0.1912 | 0.0594 | 0.6159 | 0.5945 |
| 2 | 4_TUTI | 2 | 0 | 97.15 | 35.951 | 0.1912 | 0.0594 | 0.6159 | 0.5945 |
| 1 | 4_CARW | 1 | 0 | 212.44 | 98.180 | 0.1337 | 0.0867 | 0.2061 | 0.2112 |
| 2 | 4_CACH | 1 | 0 | 91.98 | 59.727 | 0.1151 | 0.0423 | 0.3129 | 0.4948 |
| 1 | 4_AMCR | 1 | 0 | 238.39 | 164.609 | 0.0797 | 0.0525 | 0.1210 | 0.2025 |

**Transect 5**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 5_ALL | 1 | 0 | 499.40 | 23.841 | 4.4042 | 2.0620 | 9.4066 | 0.2819 |
| 1 | 5_CARW | 1 | 0 | 101.45 | 30.832 | 0.7568 | 0.3597 | 1.5923 | 0.3574 |
| 2 | 5_NOCA | 1 | 0 | 107.37 | 44.690 | 0.4848 | 0.2401 | 0.9789 | 0.3171 |
| 1 | 5_WEVI | 1 | 0 | 143.69 | 55.362 | 0.4817 | 0.0692 | 3.3532 | 0.5725 |
| 2 | 5_BGGN | 1 | 0 | 40.80 | 25.351 | 0.3945 | 0.0680 | 2.2893 | 0.7992 |
| 2 | 5_BARS | 1 | 0 | 43.16 | 61.277 | 0.1360 | 0.0061 | 3.0478 | 1.0578 |
| 1 | 5_AMCR | 1 | 0 | 134.30 | 161.406 | 0.1239 | 0.0358 | 0.4292 | 0.4407 |

**Transect 6**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 6_ALL | 2 | 0 | 856.72 | 21.186 | 3.9334 | 2.6262 | 5.8913 | 0.2010 |
| 1 | 6_NOCA | 1 | 0 | 219.60 | 42.530 | 0.5094 | 0.2350 | 1.1046 | 0.3399 |
| 1 | 6_WEVI | 1 | 0 | 172.60 | 38.177 | 0.4584 | 0.1411 | 1.4892 | 0.5147 |
| 2 | 6_BGGN | 1 | 0 | 85.66 | 23.726 | 0.4566 | 0.0973 | 2.1425 | 0.7370 |
| 2 | 6_CARW | 2 | 0 | 220.86 | 61.547 | 0.3114 | 0.1338 | 0.7248 | 0.4139 |
| 1 | 6_AMCR | 1 | 0 | 290.75 | 139.113 | 0.1617 | 0.0964 | 0.2713 | 0.2424 |
| 2 | 6_MODO | 1 | 0 | 98.40 | 79.992 | 0.1146 | 0.0383 | 0.3429 | 0.5186 |
| 2 | 6_YRWA | 1 | 0 | 29.21 | 29.997 | 0.1111 | 0.0134 | 0.9232 | 1.1003 |

**Transect 7**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 7_ALL | 2 | 0 | 609.68 | 15.513 | 6.0434 | 3.5463 | 10.2989 | 0.2725 |
| 1 | 7_WEVI | 1 | 0 | 131.72 | 22.540 | 0.9982 | 0.3739 | 2.6649 | 0.4362 |
| 1 | 7_NOCA | 1 | 0 | 193.31 | 40.306 | 0.7133 | 0.3815 | 1.3338 | 0.2537 |
| 1 | 7_CARW | 1 | 0 | 236.95 | 61.409 | 0.5496 | 0.3875 | 0.7795 | 0.1718 |
| 2 | 7_CACH | 1 | 0 | 62.41 | 42.813 | 0.2336 | 0.0642 | 0.8496 | 0.6317 |
| 2 | 7_RBWO | 1 | 0 | 78.43 | 101.094 | 0.0989 | 0.0355 | 0.2756 | 0.4520 |
| 1 | 7_AMCR | 1 | 0 | 134.49 | 309.296 | 0.0445 | 0.0244 | 0.0811 | 0.2808 |

**Transect 8**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 8_ALL | 2 | 0 | 1183.53 | 44.248 | 2.4107 | 1.4829 | 3.9188 | 0.2385 |
| 1 | 8_NOCA | 1 | 0 | 276.77 | 65.989 | 0.3662 | 0.1747 | 0.7675 | 0.3196 |
| 2 | 8_CARW | 2 | 0 | 204.45 | 76.615 | 0.2175 | 0.1061 | 0.4459 | 0.3388 |
| 2 | 8_WEVI | 2 | 0 | 110.92 | 48.121 | 0.2078 | 0.0458 | 0.9421 | 0.7302 |
| 2 | 8_BGGN | 1 | 0 | 77.58 | 49.303 | 0.1521 | 0.0535 | 0.4327 | 0.4860 |
| 2 | 8_AMCR | 1 | 0 | 299.68 | 208.815 | 0.1038 | 0.0690 | 0.1561 | 0.2003 |
| 2 | 8_AMRO | 1 | 0 | 38.29 | 93.355 | 0.0357 | 0.0042 | 0.3020 | 1.1362 |
| 2 | 8_BHCO | 1 | 0 | 39.54 | 94.088 | 0.0354 | 0.0063 | 0.1989 | 0.8510 |

**Transect 9**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 9_ALL | 2 | 0 | 1052.21 | 23.672 | 3.7114 | 2.4488 | 5.6250 | 0.2119 |
| 1 | 9_NOCA | 2 | 0 | 330.31 | 26.898 | 1.0888 | 0.7441 | 1.5930 | 0.1857 |
| 1 | 9_WEVI | 1 | 0 | 225.56 | 45.563 | 0.4076 | 0.1263 | 1.3153 | 0.5211 |
| 1 | 9_CARW | 1 | 0 | 209.20 | 44.641 | 0.3840 | 0.2490 | 0.5923 | 0.2110 |
| 2 | 9_CACH | 1 | 0 | 83.90 | 39.604 | 0.1804 | 0.0607 | 0.5360 | 0.5328 |
| 1 | 9_AMCR | 1 | 0 | 321.36 | 132.631 | 0.1616 | 0.0734 | 0.3556 | 0.3483 |

**Transect 10**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 10_ALL | 1 | 0 | 402.41 | 57.180 | 1.0493 | 0.3520 | 3.1284 | 0.4442 |
| 1 | 10_WEVI | 1 | 0 | 82.74 | 28.188 | 0.4878 | 0.0760 | 3.1300 | 0.7252 |
| 1 | 10_CARW | 1 | 0 | 118.81 | 59.007 | 0.2966 | 0.1211 | 0.7264 | 0.4301 |
| 2 | 10_NOCA | 1 | 0 | 113.44 | 57.151 | 0.2843 | 0.0967 | 0.8358 | 0.4464 |
| 2 | 10_AMCR | 1 | 0 | 79.72 | 74.993 | 0.1500 | 0.0565 | 0.3982 | 0.4360 |

**Transect 11**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 11_ALL | 1 | 0 | 768.41 | 47.027 | 1.3063 | 0.7373 | 2.3143 | 0.2579 |
| 2 | 11_CARW | 1 | 0 | 75.44 | 21.884 | 0.3590 | 0.1348 | 0.9564 | 0.4880 |
| 1 | 11_WEVI | 1 | 0 | 145.52 | 50.660 | 0.2256 | 0.1044 | 0.4876 | 0.3546 |
| 2 | 11_BGGN | 1 | 0 | 63.22 | 29.997 | 0.2143 | 0.0607 | 0.7562 | 0.6144 |
| 1 | 11_NOCA | 1 | 0 | 174.45 | 77.256 | 0.1664 | 0.0542 | 0.5106 | 0.5177 |
| 2 | 11_MODO | 1 | 0 | 139.65 | 82.141 | 0.1304 | 0.0495 | 0.3436 | 0.4526 |
| 1 | 11_AMCR | 1 | 0 | 232.33 | 154.463 | 0.1017 | 0.0579 | 0.1788 | 0.2715 |

**Transect 12**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 12_ALL | 2 | 0 | 1625.90 | 78.077 | 1.1242 | 0.6639 | 1.9037 | 0.2491 |
| 2 | 12_FISP | 2 | 0 | 70.50 | 20.940 | 0.2388 | 0.0469 | 1.2144 | 0.8490 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 12_WTSP | 1 | 0 | 34.50 | 15.000 | 0.2222 | 0.0409 | 1.2078 | 0.8849 |
| 2 | 12_NOCA | 1 | 0 | 128.00 | 51.276 | 0.1734 | 0.0613 | 0.4905 | 0.5319 |
| 2 | 12_CLSW | 1 | 0 | 83.03 | 38.786 | 0.1432 | 0.0316 | 0.6492 | 0.7531 |
| 2 | 12_BARS | 1 | 0 | 73.31 | 34.920 | 0.1432 | 0.0289 | 0.7093 | 0.8057 |
| 1 | 12_CARW | 1 | 0 | 343.17 | 127.266 | 0.1397 | 0.0856 | 0.2280 | 0.2277 |
| 2 | 12_SOSP | 1 | 0 | 36.01 | 29.997 | 0.0926 | 0.0215 | 0.3986 | 0.7526 |
| 2 | 12_NOMO | 1 | 0 | 95.02 | 118.873 | 0.0421 | 0.0137 | 0.1290 | 0.5423 |
| 1 | 12_WEVI | 1 | 0 | 155.29 | 188.547 | 0.0413 | 0.0156 | 0.1094 | 0.4748 |
| 2 | 12_EAME | 1 | 0 | 65.79 | 95.249 | 0.0408 | 0.0133 | 0.1252 | 0.5554 |
| 1 | 12_AMCR | 1 | 0 | 245.48 | 307.119 | 0.0380 | 0.0179 | 0.0808 | 0.3731 |
| 2 | 12_MODO | 1 | 0 | 84.76 | 121.693 | 0.0365 | 0.0124 | 0.1079 | 0.5253 |
| 1 | 12_RBWO | 1 | 0 | 150.75 | 212.345 | 0.0340 | 0.0158 | 0.0732 | 0.3710 |
| 2 | 12_CEDW | | | | | 0.0216 | 0.0032 | 0.1474 | 1.0000 |
| 2 | 12_RWBL | 1 | 0 | 40.01 | 115.686 | 0.0192 | 0.0028 | 0.1339 | 1.0605 |
| 2 | 12_VESP | | | | | 0.0074 | 0.0011 | 0.0505 | 1.0000 |

**Transect 13**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 13_ALL | 5 | 0 | 1467.22 | 53.962 | 1.8664 | 1.1681 | 2.9820 | 0.2078 |
| 2 | 13_LISP | 1 | 0 | 27.51 | 4.924 | 1.1605 | 0.2228 | 6.0453 | 0.8333 |
| 2 | 13_NOCA | 2 | 0 | 130.31 | 35.480 | 0.2819 | 0.1456 | 0.5456 | 0.3145 |
| 1 | 13_CARW | 1 | 0 | 135.97 | 44.410 | 0.2413 | 0.1215 | 0.4789 | 0.3262 |
| 2 | 13_MODO | 2 | 0 | 123.83 | 49.994 | 0.1857 | 0.0695 | 0.4961 | 0.4847 |
| 1 | 13_AMCR | 2 | 0 | 394.32 | 136.239 | 0.1835 | 0.1071 | 0.3143 | 0.2592 |
| 2 | 13_CACH | 1 | 0 | 108.45 | 59.994 | 0.1548 | 0.0675 | 0.3548 | 0.3961 |
| 1 | 13_WEVI | 1 | 0 | 132.44 | 66.026 | 0.1515 | 0.0476 | 0.4815 | 0.5192 |
| 2 | 13_AMRO | 1 | 0 | 67.50 | 68.205 | 0.0733 | 0.0195 | 0.2762 | 0.6285 |
| 2 | 13_EAME | 1 | 0 | 37.50 | 84.560 | 0.0338 | 0.0064 | 0.1794 | 0.8366 |

**Transect 14**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 14_ALL | 3 | 0 | 973.92 | 58.005 | 1.4798 | 0.7861 | 2.7854 | 0.3028 |
| 1 | 14_CARW | 1 | 0 | 185.40 | 64.923 | 0.2567 | 0.1399 | 0.4711 | 0.2799 |
| 2 | 14_YRWA | 1 | 0 | 86.47 | 37.705 | 0.2431 | 0.0295 | 2.0022 | 1.0432 |
| 1 | 14_NOCA | 1 | 0 | 160.70 | 69.419 | 0.2041 | 0.0668 | 0.6234 | 0.4868 |
| 1 | 14_AMCR | 1 | 0 | 265.16 | 253.806 | 0.0722 | 0.0466 | 0.1120 | 0.2074 |
| 2 | 14_CLSW | 1 | 0 | 51.39 | 104.094 | 0.0400 | 0.0048 | 0.3314 | 1.0372 |
| 2 | 14_SNEG | | | | | 0.0042 | 0.0005 | 0.0354 | 1.0000 |

**Transect 15**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 15_ALL | 3 | 0 | 1161.66 | 31.558 | 3.1009 | 1.0833 | 8.8763 | 0.5707 |
| 1 | 15_NOCA | 2 | 0 | 380.25 | 40.519 | 0.7580 | 0.4493 | 1.2788 | 0.2488 |
| 2 | 15_CARW | 1 | 0 | 186.98 | 55.773 | 0.2946 | 0.1043 | 0.8318 | 0.5091 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 15_CACH | 1 | 0 | 128.32 | 37.517 | 0.2856 | 0.1467 | 0.5561 | 0.3125 |
| 2 | 15_BGGN | 1 | 0 | 87.33 | 34.991 | 0.2450 | 0.0422 | 1.4206 | 0.9188 |
| 1 | 15_WEVI | 1 | 0 | 112.18 | 40.631 | 0.2285 | 0.0609 | 0.8583 | 0.6193 |
| 2 | 15_AMCR | 2 | 0 | 185.34 | 67.874 | 0.1894 | 0.0673 | 0.5332 | 0.5204 |
| 2 | 15_PABU | 1 | 0 | 178.49 | 85.750 | 0.1583 | 0.0367 | 0.6834 | 0.6826 |
| 2 | 15_BHCO | 1 | 0 | 60.43 | 45.119 | 0.1108 | 0.0304 | 0.4034 | 0.6341 |
| 2 | 15_DICK | 1 | 0 | 61.48 | 69.992 | 0.0714 | 0.0094 | 0.5419 | 1.0548 |
| 2 | 15_MODO | 1 | 0 | 93.71 | 163.188 | 0.0394 | 0.0137 | 0.1135 | 0.5171 |

**Transect 16**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 16_ALL | 2 | 0 | 1820.86 | 83.511 | 1.7363 | 1.2713 | 2.3715 | 0.1554 |
| 1 | 16_CARW | 2 | 0 | 233.44 | 93.804 | 0.1954 | 0.1033 | 0.3697 | 0.3019 |
| 1 | 16_NOCA | 1 | 0 | 93.62 | 54.307 | 0.1534 | 0.0842 | 0.2796 | 0.2824 |
| 2 | 16_BARS | 2 | 0 | 75.02 | 45.008 | 0.1481 | 0.0225 | 0.9754 | 0.9427 |
| 2 | 16_PABU | 2 | 0 | 134.90 | 79.103 | 0.1370 | 0.0191 | 0.9810 | 0.9544 |
| 1 | 16_AMCR | 1 | 0 | 483.48 | 277.480 | 0.1201 | 0.0731 | 0.1974 | 0.2262 |
| 2 | 16_DICK | 1 | 0 | 38.89 | 40.000 | 0.1042 | 0.0126 | 0.8579 | 1.0541 |
| 2 | 16_CACH | 1 | 0 | 79.54 | 74.253 | 0.1010 | 0.0285 | 0.3575 | 0.6258 |
| 2 | 16_BAOR | 1 | 0 | 82.59 | 87.991 | 0.0852 | 0.0103 | 0.7042 | 1.0377 |
| 2 | 16_BHCO | 1 | 0 | 159.69 | 154.065 | 0.0811 | 0.0241 | 0.2729 | 0.5441 |
| 2 | 16_MODO | 1 | 0 | 103.90 | 131.414 | 0.0634 | 0.0323 | 0.1246 | 0.3228 |
| 2 | 16_WEVI | 1 | 0 | 117.16 | 158.257 | 0.0579 | 0.0180 | 0.1860 | 0.5389 |
| 1 | 16_BLJA | 1 | 0 | 155.52 | 240.539 | 0.0485 | 0.0199 | 0.1182 | 0.4283 |
| 2 | 16_RBWO | 1 | 0 | 178.43 | 272.756 | 0.0458 | 0.0252 | 0.0835 | 0.2917 |
| 2 | 16_CAEG | 1 | 0 | 70.20 | 263.987 | 0.0189 | 0.0039 | 0.0930 | 0.7707 |
| 2 | 16_SNEG | | | | | 0.0064 | 0.0008 | 0.0545 | 1.0000 |

**SUPPLEMENT 5**

**Inventory of Bird Species Observed at Camp Mabry, Austin, Texas**

**20 September 2003–20 November 2004**

| Code | Common Name | Scientific Name |
|---|---|---|
| AMCR | American Crow | *Corvus brachyrhynchos* |
| AMGO | American Goldfinch | *Carduelis tristis* |
| AMKE | American Kestrel | *Falco sparverius* |
| AMRE | American Redstart | *Setophaga ruticilla* |
| AMRO | American Robin | *Turdus migratorius* |
| BARS | Barn Swallow | *Hirundo rustica* |
| BBWD | Black-bellied Whistling-Duck | *Dendrocygna autumnalis* |
| BCHU | Black-chinned Hummingbird | *Archilochus alexandri* |
| BCTI | Black-crested Titmouse | *Baeolophus atricristatus* |
| BEKI | Belted Kingfisher | *Ceryle alcyon* |
| BEWR | Bewick's Wren | *Thryomanes bewickii* |
| BGGN | Blue-gray Gnatcatcher | *Polioptila caerulea* |
| BHCO | Brown-headed Cowbird | *Molothrus ater* |
| BHVI | Blue-headed Vireo | *Vireo solitarius* |
| BLJA | Blue Jay | *Cyanocitta cristata* |
| BLVU | Black Vulture | *Coragyps atratus* |
| BTNW | Black-throated Green Warbler | *Dendroica virens* |
| BWHA | Broad-winged Hawk | *Buteo platypterus* |
| BWWA | Blue-winged Warbler | *Vermivora pinus* |
| CACH | Carolina Chickadee | *Poecile carolinensis* |
| CANW | Canyon Wren | *Catherpes mexicanus* |
| CARW | Carolina Wren | *Thryothorus ludovicianus* |
| CEDW | Cedar Waxwing | *Bombycilla cedrorum* |
| CERW | Cerulean Warbler | *Dendroica cerulea* |
| CHSP | Chipping Sparrow | *Spizella passerina* |
| CHSW | Chimney Swift | *Chaetura pelagica* |
| CLSW | Cliff Swallow | *Petrochelidon pyrrhonota* |
| COGR | Common Grackle | *Quiscalus quiscula* |
| COHA | Cooper's Hawk | *Accipiter cooperii* |
| CWWI | Chuck-will's-widow | *Caprimulgus carolinensis* |

| | | |
|---|---|---|
| DCCO | Double-crested Cormorant | *Phalacrocorax auritus* |
| DICK | Dickcissel | *Spiza americana* |
| DOWO | Downy Woodpecker | *Picoides pubescens* |
| EAME | Eastern Meadowlark | *Sturnella magna* |
| EAPH | Eastern Phoebe | *Sayornis phoebe* |
| EASO | Eastern Screech-Owl | *Megascops asio* |
| FISP | Field Sparrow | *Spizella pusilla* |
| FOSP | Fox Sparrow | *Passerella iliaca* |
| GBHE | Great Blue Heron | *Ardea herodias* |
| GCFL | Great Crested Flycatcher | *Myiarchus crinitus* |
| GCKI | Golden-crowned Kinglet | *Regulus satrapa* |
| GCWA | Golden-cheeked Warbler | *Dendroica chrysoparia* |
| GREG | Great Egret | *Ardea alba* |
| GRHE | Green Heron | *Butorides virescens* |
| HERG | Herring Gull | *Larus argentatus* |
| HOFI | House Finch | *Carpodacus mexicanus* |
| HOSP | House Sparrow | *Passer domesticus* |
| HOWR | House Wren | *Troglodytes aedon* |
| INBU | Indigo Bunting | *Passerina cyanea* |
| KILL | Killdeer | *Charadrius vociferus* |
| LAGU | Laughing Gull | *Larus atricilla* |
| LBWO | Ladder-backed Woodpecker | *Picoides scalaris* |
| LEGO | Lesser Goldfinch | *Carduelis psaltria* |
| LESC | Lesser Scaup | *Aythya affinis* |
| LISP | Lincoln's Sparrow | *Melospiza lincolnii* |
| LOSH | Loggerhead Shrike | *Lanius ludovicianus* |
| MODO | Mourning Dove | *Zenaida macroura* |
| NAWA | Nashville Warbler | *Vermivora ruficapilla* |
| NOCA | Northern Cardinal | *Cardinalis cardinalis* |
| NOFL | Northern Flicker | *Colaptes auratus* |
| NOMO | Northern Mockingbird | *Mimus polyglottos* |
| NOPA | Northern Parula | *Parula americana* |
| OCWA | Orange-crowned Warbler | *Vermivora celata* |
| PABU | Painted Bunting | *Passerina ciris* |
| PBGR | Pied-billed Grebe | *Podilymbus podiceps* |
| PIWA | Pine Warbler | *Dendroica pinus* |
| PIWO | Pileated Woodpecker | *Dryocopus pileatus* |
| PUMA | Purple Martin | *Progne subis* |
| RBGR | Rose-breasted Grosbeak | *Pheucticus ludovicianus* |
| RBGU | Ring-billed Gull | *Larus delawarensis* |
| RBWO | Red-bellied Woodpecker | *Melanerpes carolinus* |

| | | |
|---|---|---|
| RCKI | Ruby-crowned Kinglet | *Regulus calendula* |
| REVI | Red-eyed Vireo | *Vireo olivaceus* |
| RNDU | Ring-necked Duck | *Aythya collaris* |
| RSHA | Red-shouldered Hawk | *Buteo lineatus* |
| RTHA | Red-tailed Hawk | *Buteo jamaicensis* |
| RTHU | Ruby-throated Hummingbird | *Archilochus colubris* |
| RWBL | Red-winged Blackbird | *Agelaius phoeniceus* |
| SAVS | Savannah Sparrow | *Passerculus sandwichensis* |
| SNEG | Snowy Egret | *Egretta thula* |
| SPTO | Spotted Towhee | *Pipilo maculatus* |
| SSHA | Sharp-shinned Hawk | *Accipiter striatus* |
| STFL | Scissor-tailed Flycatcher | *Tyrannus forficatus* |
| SUTA | Summer Tanager | *Piranga rubra* |
| TUTI | Tufted Titmouse | *Baeolophus bicolor* |
| TUVU | Turkey Vulture | *Cathartes aura* |
| UPSA | Upland Sandpiper | *Bartramia longicauda* |
| VESP | Vesper Sparrow | *Pooecetes gramineus* |
| WCSP | White-crowned Sparrow | *Zonotrichia leucophrys* |
| WEKI | Western Kingbird | *Tyrannus verticalis* |
| WEVI | White-eyed Vireo | *Vireo griseus* |
| WFIB | White-faced Ibis | *Plegadis chihi* |
| WODU | Wood Duck | *Aix sponsa* |
| WOTH | Wood Thrush | *Hylocichla mustelina* |
| WTSP | White-throated Sparrow | *Zonotrichia albicollis* |
| WWDO | White-winged Dove | *Zenaida asiatica* |
| YBCH | Yellow-breasted Chat | *Icteria virens* |
| YBCU | Yellow-billed Cuckoo | *Coccyzus americanus* |
| YRWA | Yellow-rumped Warbler | *Dendroica coronata* |
| YWAR | Yellow Warbler | *Dendroica petechia* |

**SUPPLEMENT 6**

## Partners in Flight Species of Concern

Texas Oaks and Prairies Region (grasslands and scrub habitats)

| | Scientific Name | Present at Camp Mabry? | Likely at Camp Mabry |
|---|---|---|---|
| Bewick's Wren (Eastern subspecies, winter only) | *Thryomanes bewickii* | Yes | Yes |
| Scissor-tailed Flycatcher | *Tyrannus forficatus* | Yes | Yes |
| Painted Bunting | *Passerina ciris* | Yes | Yes |
| Bell's Vireo | *Vireo bellii* | No | Unlikely |
| Northern Bobwhite | *Colinus virginianus* | No | Unlikely |

Edwards Plateau (Juniper-mesquite savannah and brushlands)

| | Scientific Name | Present at Camp Mabry? | Likely at Camp Mabry |
|---|---|---|---|
| Golden-cheeked Warbler (highest percent population of any physiographic area) | *Dendroica chrysoparia* | Yes | Probably only during migration |
| Black-capped Vireo (highest percent population of any physiographic area) | *Vireo atricapilla* | No | No |
| Bell's Vireo | *Vireo bellii* | No | No |
| Painted Bunting | *Passerina ciris* | Yes | Yes |
| Black-chinned Hummingbird | *Archilocus alexandri* | Yes | Yes |
| Rufous-crowned Sparrow | *Aimophila ruficeps* | No | Possible |
| Cave Swallow | *Petrochelidon fulva* | Yes | Yes |
| Scissor-tailed Flycatcher | *Tyrannus forficatus* | Yes | Yes |
| Canyon Towhee | *Pipilo fuscus* | No | Unlikely |
| Cassin's Sparrow | *Aimophila cassinii* | No | No |
| Orchard Oriole | *Icterus spurius* | No | Unlikely |
| Northern Bobwhite | *Colinus virginianus* | No | No |

| **PIF Species with Multiple Causes for Concern Across Their Entire Range** | | | |
|---|---|---|---|
| Common Name | Scientific Name | Observed at Camp Mabry? | Likely to Be at Camp Mabry? |
| Black-capped Vireo | *Vireo atricapilla* | No | No |
| Golden-cheeked Warbler | *Dendroica chrysoparia* | Yes | Unlikely; migrant status |
| **PIF Species that are Moderately Abundant or Widespread with Declines or High Threats** | | | |
| Common Name | Scientific Name | Observed at Camp Mabry? | Likely to Be at Camp Mabry? |
| Swainson's Hawk | *Buteo swainsoni* | Yes | Unlikely |
| Bell's Vireo | *Vireo atricapilla* | No | No |
| Brown-headed Nuthatch | *Sitta pusilla* | No | No |
| Wood Thrush | *Hylocichla mustelina* | Yes | Migrant |
| Prothonotary Warbler | *Protonotaria citrea* | No | Migrant |
| Worm-eating Warbler | *Helmitheros vermivorum* | No | Migrant |
| Kentucky Warbler | *Oporornis formosus* | No | Migrant |
| Harris's Sparrow | *Zonotrichia querula* | Yes | Migrant |
| Painted Bunting | *Passerina ciris* | Yes | Yes |
| Dickcissel | *Spiza americana* | Yes | Migrant |

**SUPPLEMENT 7**

**Species Listed by State and Federal Authorities That Breed or Overwinter in the Camp Mabry Region**

| Songbirds | State Status | Federal Status |
|---|---|---|
| Black-capped Vireo (*Vireo atricapillus*) | Endangered | Endangered |
| Golden-cheeked Warbler (*Dendroica chrysoparia*) | Endangered | Endangered |

**SUPPLEMENT 8**

## Distance 4.1 raw data for all species observed at Camp Mabry with 10 or more registrations

Key to abbreviations
Status: 1 – ran with no constrained variables, 2 – ran with some constraints
Name: 4-letter species abbreviation, or all (for all bird species)
Delta AIC: minimum AIC, calculated within survey and data filter
AIC: Akaike Information Criterion value
ESW: Effective strip width
D: Density of individuals (per hectares)
D LCL: Density of individuals analytic lower confidence limit
D UCL: Density of individuals analytic upper confidence limit
D CV: Density of individuals analytic coefficient of variation

### All of Mabry

| Status | Name | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|
| 1 | NOCA | 0 | 1998.121 | 33.78219 | 0.4600699 | 0.3717748 | 0.5693347 | 0.1085 |
| 1 | CARW | 0 | 1757.995 | 41.82513 | 0.3053448 | 0.2422447 | 0.3848812 | 0.1178 |
| 1 | DOWO | 0 | 1636.888 | 40.64545 | 0.2919753 | 0.2310879 | 0.3689054 | 0.119 |
| 1 | RCKI | 0 | 1052.813 | 29.90115 | 0.2639218 | 0.186677 | 0.3731296 | 0.1762 |
| 1 | BLJA | 0 | 2207.195 | 70.69831 | 0.2019441 | 0.1659081 | 0.2458074 | 0.0997 |
| 1 | CACH | 0 | 1164.594 | 47.43996 | 0.1726977 | 0.1338304 | 0.2228529 | 0.1295 |
| 1 | NOMO | 0 | 1394.372 | 58.40276 | 0.1526583 | 0.1178661 | 0.1977205 | 0.1314 |
| 1 | HOFI | 0 | 747.3953 | 39.13214 | 0.1339299 | 9.47E-02 | 0.1894516 | 0.1764 |
| 1 | YRWA | 0 | 233.9716 | 19.02903 | 0.1076352 | 5.71E-02 | 0.2028181 | 0.3278 |
| 1 | BGGN | 0 | 163.1975 | 23.00901 | 6.28E-02 | 3.02E-02 | 0.1305317 | 0.3816 |
| 1 | RBWO | 0 | 839.5594 | 88.48316 | 5.58E-02 | 4.05E-02 | 7.70E-02 | 0.1639 |
| 1 | WEVI | 0 | 418.9379 | 55.18968 | 5.13E-02 | 3.17E-02 | 8.29E-02 | 0.2464 |
| 1 | AMCR | 0 | 1079.084 | 131.964 | 4.47E-02 | 3.20E-02 | 6.26E-02 | 0.1712 |
| 1 | LEGO | 0 | 238.253 | 41.27336 | 4.09E-02 | 2.08E-02 | 8.01E-02 | 0.3494 |
| 1 | NAWA | 0 | 152.9046 | 32.52485 | 3.52E-02 | 1.32E-02 | 9.36E-02 | 0.5244 |
| 1 | CHSW | 0 | 230.6457 | 56.45839 | 2.88E-02 | 1.51E-02 | 5.51E-02 | 0.3353 |
| 1 | MODO | 0 | 180.9642 | 48.92793 | 2.83E-02 | 1.21E-02 | 6.64E-02 | 0.443 |
| 1 | BEWR | 0 | 344.2807 | 80.94457 | 2.60E-02 | 1.68E-02 | 0.0404754 | 0.2252 |
| 1 | AMRO | 0 | 109.3418 | 33.1873 | 2.54E-02 | 1.12E-02 | 0.0577363 | 0.4312 |
| 1 | TUTI | 0 | 268.2701 | 69.28156 | 2.52E-02 | 0.0134258 | 0.0473592 | 0.3262 |
| 1 | PUMA | 0 | 202.2498 | 55.99467 | 2.26E-02 | 0.0122141 | 4.18E-02 | 0.3168 |
| 1 | BARS | 0 | 125.203 | 50.91749 | 1.66E-02 | 7.81E-03 | 0.0351363 | 0.391 |
| 1 | COGR | 0 | 163.7673 | 67.40887 | 1.52E-02 | 7.19E-03 | 3.21E-02 | 0.3908 |
| 1 | DICK | 0 | 86.19421 | 49.44873 | 1.22E-02 | 4.12E-03 | 3.60E-02 | 0.5861 |
| 1 | KILL | 0 | 167.9725 | 128.6614 | 7.49E-03 | 3.97E-03 | 1.41E-02 | 0.3262 |
| 1 | RBGU | 0 | 134.9021 | 105.2785 | 7.44E-03 | 3.05E-03 | 1.81E-02 | 0.4718 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 2 | GBHE | 0 | 80.51208 | 79.08953 | 6.09E-03 | 2.75E-03 | 1.35E-02 | 0.4114 |
| 2 | TUVU | 0 | 86.80438 | 130.2104 | 3.70E-03 | 1.18E-03 | 1.16E-02 | 0.5929 |
| 1 | RTHA | 0 | 132.6028 | 251.066 | 2.64E-03 | 1.31E-03 | 5.33E-03 | 0.3635 |

**Transect 1**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 1 | 0 | 1103.508 | 18.0117 | 3.83589 | 2.636794 | 5.580282 | 0.1904 |
| 1 | RCKI | 1 | 0 | 99.59946 | 5.255195 | 1.470406 | 0.5542292 | 3.901085 | 0.5024 |
| 1 | NOCA | 1 | 0 | 486.1357 | 48.08227 | 0.5483027 | 0.3917862 | 0.7673466 | 0.167 |
| 1 | BLJA | 1 | 0 | 556.671 | 64.81187 | 0.4207983 | 0.3076345 | 0.5755897 | 0.1523 |
| 2 | CARW | 1 | 0 | 338.434 | 50 | 0.3909091 | 0.2414253 | 0.632949 | 0.2355 |
| 1 | CACH | 1 | 0 | 185.4554 | 33.6596 | 0.3105963 | 0.1718614 | 0.5613247 | 0.2957 |
| 2 | COGR | 2 | 0 | 97.77037 | 26.84798 | 0.2031641 | 6.04E-02 | 0.6836975 | 0.605 |
| 2 | YRWA | 2 | 0 | 144.5948 | 49.7087 | 0.1463069 | 6.09E-02 | 0.3514062 | 0.4428 |
| 2 | HOFI | 1 | 0 | 111.3437 | 43.99751 | 0.1446363 | 3.55E-02 | 0.5894205 | 0.7299 |
| 1 | BCTI | 1 | 0 | 244.4321 | 84.55185 | 0.1343984 | 7.23E-02 | 0.2498541 | 0.3007 |
| 2 | RBWO | 1 | 0 | 130.945 | 99.98977 | 6.36E-02 | 3.06E-02 | 0.1324799 | 0.3658 |

**Transect 2**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 4 | 0 | 2824.313 | 49.34848 | 3.110532 | 2.340504 | 4.133898 | 0.1311 |
| 1 | RCKI | 1 | 0 | 125.3073 | 14.4015 | 0.6943724 | 0.2780176 | 1.734253 | 0.4388 |
| 1 | NOCA | 1 | 0 | 329.6537 | 32.03416 | 0.6711585 | 0.3995508 | 1.1274 | 0.2468 |
| 1 | CARW | 1 | 0 | 411.6071 | 65.70072 | 0.3348517 | 0.2150531 | 0.5213861 | 0.2087 |
| 1 | CACH | 1 | 0 | 153.4 | 57.15993 | 0.1487056 | 7.34E-02 | 0.3011577 | 0.3419 |
| 2 | HOFI | 1 | 0 | 103.7098 | 49.18969 | 0.1321415 | 0.0357869 | 0.4879265 | 0.6591 |
| 2 | AMCR | 2 | 0 | 123.3166 | 72.92433 | 8.23E-02 | 2.98E-02 | 0.2273818 | 0.5143 |
| 2 | NOMO | 1 | 0 | 95.70343 | 108.3289 | 4.62E-02 | 1.71E-02 | 0.1246887 | 0.492 |
| 1 | RBWO | 1 | 0 | 111.0133 | 182.6589 | 2.74E-02 | 1.19E-02 | 6.31E-02 | 0.4136 |

**Transect 3**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 5 | 0 | 3506.848 | 54.31201 | 2.823194 | 2.171709 | 3.670117 | 0.1239 |
| 1 | NOCA | 1 | 0 | 475.2855 | 48.61508 | 0.4628194 | 0.3154106 | 0.6791203 | 0.1814 |
| 1 | CARW | 2 | 0 | 388.5713 | 40.79189 | 0.4494357 | 0.3121923 | 0.6470129 | 0.182 |
| 1 | BLJA | 2 | 0 | 519.0604 | 95.15025 | 0.2145729 | 0.1449266 | 0.3176887 | 0.194 |
| 1 | CACH | 1 | 0 | 177.7909 | 42.93773 | 0.2037835 | 0.1090138 | 0.3809399 | 0.305 |
| 1 | RCKI | 1 | 0 | 160.3144 | 41.91596 | 0.18887 | 8.43E-02 | 0.4229444 | 0.3927 |
| 2 | NOMO | 1 | 0 | 208.9841 | 65.70907 | 0.152186 | 8.32E-02 | 0.2783464 | 0.3012 |
| 2 | MODO | 2 | 0 | 86.23361 | 31.48312 | 0.132346 | 5.09E-02 | 0.3438184 | 0.4802 |
| 2 | BEWR | 2 | 0 | 109.9011 | 43.44667 | 0.1150836 | 4.39E-02 | 0.3014643 | 0.489 |
| 1 | HOFI | 1 | 0 | 148.0907 | 63.68399 | 0.1046836 | 4.00E-02 | 0.2742008 | 0.4709 |
| 1 | RBWO | 1 | 0 | 147.038 | 111.5269 | 5.23E-02 | 2.75E-02 | 9.95E-02 | 0.3116 |
| 2 | AMCR | 1 | 0 | 132.2787 | 149.9828 | 3.61E-02 | 1.51E-02 | 8.62E-02 | 0.4286 |

**Transect 4**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 5 | 0 | 1916.125 | 32.67899 | 2.562809 | 1.957898 | 3.354612 | 0.1324 |
| 1 | NOCA | 1 | 0 | 484.3313 | 33.81215 | 0.7147332 | 0.3920924 | 1.302865 | 0.2866 |
| 1 | NOMO | 2 | 0 | 208.6257 | 29.5273 | 0.3527809 | 0.1907008 | 0.6526159 | 0.3035 |
| 1 | CARW | 1 | 0 | 404.9832 | 54.61101 | 0.350967 | 0.227007 | 0.5426171 | 0.2128 |
| 1 | CACH | 2 | 0 | 258.9162 | 36.72826 | 0.3403374 | 0.2014003 | 0.5751209 | 0.2627 |
| 1 | RCKI | 1 | 0 | 139.1865 | 27.18475 | 0.2912172 | 0.1193707 | 0.7104546 | 0.4389 |
| 1 | WEVI | 2 | 0 | 193.9915 | 46.2454 | 0.189208 | 8.22E-02 | 0.4355124 | 0.4074 |
| 1 | LEGO | 1 | 0 | 172.9921 | 45.95635 | 0.1813315 | 0.071015 | 0.4630164 | 0.4575 |
| 2 | YRWA | 1 | 0 | 83.81152 | 26.28099 | 0.1743973 | 5.90E-02 | 0.5153138 | 0.5355 |
| 1 | MODO | 1 | 0 | 112.8112 | 38.08862 | 0.1531516 | 6.75E-02 | 0.3473618 | 0.4127 |
| 2 | HOFI | 1 | 0 | 149.6543 | 55.56751 | 0.134971 | 6.05E-02 | 0.3011485 | 0.3997 |
| 1 | BLJA | 2 | 0 | 359.0711 | 111.3857 | 0.1234449 | 6.75E-02 | 0.2258965 | 0.2902 |
| 2 | RBWO | 2 | 0 | 91.99659 | 41.32681 | 0.1008224 | 3.62E-02 | 0.2808009 | 0.5149 |
| 2 | BEWR | 2 | 0 | 126.2485 | 59.79387 | 0.090589 | 3.31E-02 | 0.2482238 | 0.5158 |
| 2 | BCTI | 1 | 0 | 99.45211 | 66.30779 | 6.91E-02 | 2.67E-02 | 0.1789748 | 0.48 |
| 2 | CHSW | 1 | 0 | 90.53059 | 65.50486 | 6.36E-02 | 2.01E-02 | 0.2012638 | 0.584 |
| 1 | AMCR | 1 | 0 | 168.7547 | 185.0004 | 0.0337837 | 9.91E-03 | 0.1151195 | 0.6213 |

**Transect 5**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 1 | 0 | 1017.619 | 55.45437 | 1.481269 | 0.8814402 | 2.489288 | 0.231 |
| 1 | NOCA | 1 | 0 | 171.7263 | 65.90885 | 0.2059121 | 0.1064508 | 0.3983039 | 0.3191 |
| 2 | CACH | 2 | 0 | 151.7821 | 31.10723 | 0.4133168 | 0.1424565 | 1.199178 | 0.4981 |
| 1 | CARW | 1 | 0 | 168.7026 | 64.0358 | 0.2007806 | 8.91E-02 | 0.4524665 | 0.3627 |
| 1 | NOMO | 1 | 0 | 126.0025 | 74.87873 | 0.12401 | 5.00E-02 | 0.3077905 | 0.412 |
| 2 | WEVI | 2 | 0 | 93.61175 | 46.49017 | 0.1536423 | 4.52E-02 | 0.522177 | 0.5741 |
| 1 | AMCR | 1 | 0 | 153.713 | 229.6311 | 4.04E-02 | 1.61E-02 | 0.1013122 | 0.4238 |
| 1 | BLJAC | 1 | 0 | 116.9133 | 54.14338 | 0.1715023 | 5.13E-02 | 0.573581 | 0.5686 |

**Transect 6**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 3 | 0 | 4608.403 | 62.69994 | 3.763959 | 2.912188 | 4.86486 | 0.1176 |
| 1 | NOCA | 2 | 0 | 497.5676 | 58.32617 | 0.445769 | 0.3408183 | 0.5830379 | 0.1333 |
| 1 | CARW | 2 | 0 | 324.6081 | 55.67096 | 0.2963843 | 0.1498345 | 0.5862713 | 0.3325 |
| 1 | HOFI | 1 | 0 | 113.2853 | 29.96462 | 0.2669815 | 9.27E-02 | 0.7692457 | 0.5414 |
| 2 | BARS | 2 | 0 | 147.2468 | 34.00142 | 0.2499896 | 8.50E-02 | 0.735284 | 0.5271 |
| 1 | NOMO | 1 | 0 | 214.678 | 57.86544 | 0.2073777 | 0.0988957 | 0.4348572 | 0.3549 |
| 2 | COGR | 2 | 0 | 82.41896 | 26.06611 | 0.19182 | 2.88E-02 | 1.277345 | 1.0383 |
| 2 | CHSW | 2 | 0 | 114.649 | 36.32371 | 0.1789465 | 6.12E-02 | 0.5236038 | 0.5382 |
| 1 | BLJA | 1 | 0 | 296.8362 | 83.92228 | 0.1787368 | 0.1222053 | 0.2614194 | 0.1832 |
| 2 | MODO | 2 | 0 | 142.8527 | 51.68891 | 0.1450988 | 0.0649948 | 0.3239285 | 0.392 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | RBWO | 1 | 0 | 189.6998 | 73.5575 | 0.1359481 | 8.84E-02 | 0.2089668 | 0.2108 |
| 1 | RCKI | 1 | 0 | 128.5734 | 56.13705 | 0.1336016 | 4.30E-02 | 0.4154341 | 0.5641 |
| 1 | YRWA | 1 | 0 | 115.1906 | 51.97446 | 0.1250614 | 4.39E-02 | 0.3560852 | 0.5077 |
| 1 | CACH | 1 | 0 | 201.4313 | 91.88285 | 0.1088342 | 7.35E-02 | 0.1611198 | 0.1926 |
| 1 | WEVI | 1 | 0 | 108.3157 | 92.76474 | 5.93E-02 | 2.47E-02 | 0.1425622 | 0.4353 |
| 1 | AMCR | 1 | 0 | 143.7814 | 161.758 | 4.02E-02 | 1.83E-02 | 0.0881832 | 0.3829 |

**Transect 7**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 2 | 0 | 1946.895 | 52.65155 | 1.821582 | 1.417589 | 2.340706 | 0.1157 |
| 1 | NOCA | 2 | 0 | 548.4573 | 37.56475 | 0.76232 | 0.5273753 | 1.101932 | 0.1803 |
| 1 | CARW | 1 | 0 | 333.1508 | 49.47224 | 0.3491398 | 0.2142998 | 0.5688225 | 0.2326 |
| 1 | HOFI | 1 | 0 | 119.316 | 47.07584 | 0.144834 | 6.65E-02 | 0.3154581 | 0.3898 |
| 1 | BLJA | 1 | 0 | 194.3552 | 79.22161 | 0.1147529 | 6.13E-02 | 0.2149116 | 0.3028 |
| 1 | NOMO | 1 | 0 | 180.754 | 80.51836 | 0.1072596 | 5.99E-02 | 0.192063 | 0.2868 |
| 1 | WEVI | 1 | 0 | 99.64105 | 90.76208 | 5.01E-02 | 1.73E-02 | 0.1450813 | 0.528 |
| 1 | AMCR | 1 | 0 | 119.0882 | 123.8549 | 4.04E-02 | 1.89E-02 | 8.64E-02 | 0.3674 |

**Transect 8**

| Status | Name | # params | Delta AIC | AIC | ESW | D | D LCL | D UCL | D CV |
|---|---|---|---|---|---|---|---|---|---|
| 1 | ALL | 2 | 0 | 1231.92 | 57.11047 | 1.09437 | 0.6755671 | 1.772801 | 0.2274 |
| 1 | NOCA | 1 | 0 | 107.3586 | 25.18991 | 0.277889 | 0.1106188 | 0.6980942 | 0.4596 |
| 2 | CHSW | 2 | 0 | 75.36824 | 18.33667 | 0.2726776 | 0.1017592 | 0.7306767 | 0.4854 |
| 1 | BLJA | 1 | 0 | 273.1223 | 95.60224 | 0.1412101 | 8.06E-02 | 0.24748 | 0.2675 |
| 1 | NOMO | 1 | 0 | 116.2555 | 72.11379 | 8.32E-02 | 3.15E-02 | 0.2196099 | 0.4731 |
| 1 | CARW | 1 | 0 | 142.4814 | 86.03682 | 8.14E-02 | 3.90E-02 | 0.1698421 | 0.3567 |
| 2 | HOFI | 1 | 0 | 88.99557 | 61.84504 | 8.08E-02 | 0.0308654 | 0.211767 | 0.4786 |
| 1 | AMCR | 1 | 0 | 131.176 | 170.9165 | 3.51E-02 | 1.83E-02 | 0.0675182 | 0.3213 |

# Bibliography


Avise, J.C. 2000. *Phylogeography: the history and formation of species*. Cambridge, MA: Harvard University Press.

Banner, J.L. 2004. Radiogenic isotopes: systematics and applications to earth surface processes and chemical stratigraphy. *Earth-Science Reviews* 65, 141–194.

Banner, J.L., and J. Kaufman. 1994. The isotopic record of ocean chemistry and diagenesis as preserved in non-luminescent brachiopods from Missippian carbonate rocks, Illinois and Missouri. *Bulletin of the Geological Society of America* 106, 1074–1082.

Bégin, M., D.A. Roff, and V. Debat. 2004. The effect of temperature and wing morphology on quantitative genetic variation in the cricket *Gryllus firmus*, with an appendix examining the statistical properties of the Jackknife-MANOVA method of matrix comparison. *Journal of Evolutionary Biology* 17, 1255–1267.

Bibby, C.J., M. Jones, and S. Marsden. 1998. *Expedition field techniques: bird surveys*. London, UK: Royal Geographical Society.

Bibby, C.J., N.D. Burgess, D.A. Hill, and S. Mustoe. 2000. *Bird census techniques*. Second edition. San Diego, CA: Academic Press.

Bilton, D.T., J. R. Freeland, and Okamura. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32, 159–181.

Blum, J., E.H. Taliaferro, M.T Weisse, and R.T.Holmes. 2000. Changes in Sr/Ca, Ba/Ca and $^{87}Sr/^{86}Sr$ ratios between trophic levels in two forest ecosystems in the northeastern U.S.A. *Biogeochemistry* 49, 87-101.

Boivin, T., J-C Bouvier, D. Beslay, and B. Suphanor. 2004. Variability in diapause propensity within populations of a temperate insect species: interactions between insecticide resistance genes and photoperiodism. *Biological Journal of the Linnean Society* 83, 341–351.

Bowen G. J., L. I. Wassenaar, and K.A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* **143**, 337-348.

Buckland, S.T. Submitted. Point transect surveys for songbirds: robust methodologies.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2004. *Advanced distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buskirk, R.E., and K.J. Sherman. 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Florida Entomology* 68(1), 39–51.

Calvert, P.P. 1929. Different rates of growth among animals with special reference to the Odonata. *Proc. Am Ento Soc* 68(3): 227–274.

Capo, R. C. and DePaolo, D. J., 1992, Homogeneity of Sr isotopes in the oceans. *EOS, Trans. Amer. Geophys. Union*, v. 73, p. 272.

Capo, R.C., B.W. Stewart, and O.A. Chadwick. 1998. Strontium isotopes as tracers of ecosystem processes: theory and methods. *Geoderma* 82(1), 197–225.

Carter, M.F., W.C. Hunter, D.N. Pashley, and K.V. Rosenberg. 2000. Setting conservation priorities for landbirds in the United States: The Partners In Flight approach. *Auk* 117:541-548.

Case, T. 1999. *An illustrated guide to theoretical ecology*. Oxford, UK: Oxford University Press.

Catling, P.M. 2003. *Anax junius* overwintering in eastern Ontario. Pp. 9-10 in P.M. Catling, C. Jones, and P. Pratt, *eds., Ontario Odonata* vol. 4, Toronto Entomologist's Association, Toronto, Canada.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry, and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.

Chapuis, M.P., and A. Estoup. In press. Microsatellite null alleles and estimation of population differentiation. *Molecular Biology and Evolution*

Clegg, S.M., J.F. Kelly, M. Kimura, and T.B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology* 12, 819–830.

Clobert, J. 2001. Introduction. In *Dispersal,* edited by J. Clobert. New York: Oxford University Press.

Cockerham, C.C., and B.S. Weir. 1987. Correlations, descent measures: drift with migration and mutation. *Proceedings of the National Academy of Sciences* 84(23), 8512–8514.

Corbet, P.S. 1955. The immature stages of the emperor dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *Entomological Gazette* 6, 189–204.

Corbet, P.S. 1957. The life-history of the emperor dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *Journal of Animal Ecology* 26, 1–69.

Corbet, P.S. 1960. Seasonal regulation. Pp. 138–48. In P.S. Corbet, C. Longfield, and N.W. Moore, *Dragonflies*. London: Collins.

Corbet, P.S. 1962. *A biology of dragonflies*. London, UK: HF & G. Witherby.

Corbet, P.S. 1999. *Dragonflies: behavior and ecology of Odonata.* Ithaca: Cornell University Press.

Corbet, P.S. 2003. A positive correlation between photoperiod and development rate in summer species of Odonata could help to make emergence date appropriate to latitude: a testable hypothesis. *Journal of the Entomological Society of British Columbia* 100, 3–17.

Corbet, P.S., and S.A. Corbet. 1958. Emergence of a summer species of dragonfly. *Nature* 182, 194.

De Block, M., and R. Stoks. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology* 16, 986–995.

De Block, M., and R. Stoks. 2004. Life history responses depend on timing of cannibalism in a damselfly. *Freshwater Biology* 49, 775–786.

De Block, M., and R. Stoks. 2005. Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. *Oikos* 108, 485–494.

Dingle, H. 1996. *Migration: the biology of life on the move*. New York: Oxford University Press.

Dockx, C., L.P. Brower, L.I. Wassenaar, and K.A. Hobson. 2004. Do North American Monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. *Ecological Applications* 14(4), 1106–1114.

Dudley, R. 2002. *The biomechanics of insect flight*. Princeton, NJ: Princeton University Press.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software Structure: a simulation study. *Molecular Ecology* 14(8), 2611–2620.

Faure, G., and T.M. Mensing. 2005. *Isotopes: principles and applications*. Third edition. Hoboken, NJ: John Wiley & Sons.

Freeland, J.R., M. May, R. Lodge, and K.F. Conrad. 2003. Genetic diversity and widespread haplotypes in a migratory dragonfly, the common green darner (*Anax junius*). *Ecological Entomology* 28(4):413–421.

Gaggiotti, O., S.P. Brooks, W. Amos, and J. Harwood. 2004. Combining demographic, environmental and genetic data to test hypotheses about colonization events in metapopulations. *Molecular Ecology* 13(4), 811–825.

Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life-history costs and consequences in the speckled wood butterfly (*Parage aegeria)*. *Oecologia* 99: 281–289.

Hanski, I., C. Erlahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7(10), 958–966.

Harrison, R.G. 1980. Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics* 11:95–118.

Hill, J.K., and A.G. Gatehouse. 1993. Phenotypic plasticity and geographical variation in the prereproductive period of *Autographa gamma* and its implications for migration in this species. *Ecological Entomology* 18(1): 39–46.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326.

Hobson, K.A., G.J. Bowen, L.I. Wassenaar, Y. Ferrand, and H. Lormee. 2004. Using stable hydrogen and isotope measurements of feathers to infer geographical origins of European birds. *Oecologia* 141, 477–488.

Holland, R.A., M. Wikelski, and D.S. Wilcove. 2006. How and why do insects migrate? *Science* 313(5788), 794–796.

Jarvinen, O., and K. Vepsäläinen. 1975. Wing dimorphism as an adaptive strategy in water-striders (*Gerris)*. *Hereditas* 84(1): 61–68.

Jimenez, I., G.A. Londono, C.D. Cadena. 2003. Efficiency, bias, and consistency of visual and aural surveys of curassows (Cracidae) in tropical forests *J. Field Ornithol*.. 74, 210–216.

Johnson, C. G. 1960. Migration and dispersal of insects by flight. *Nature* 186, 348–350.

Jones, K.C., K.L. Levine, and J.D. Banks. 2002. Characterization of 11 polymorphic tetranucleotide microsatellites for forensic applications in California elk (*Cervus elaphus Canadensis). Molecular Ecology Notes* 2, 425–427.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M. Finch. 2002. Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130, 216–221.

Kennedy, B.P., J.D. Blum, C.L. Folt, and K.H. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences*

Kennedy, J.S. 1985. Migration, behavioral and ecological. Pp. 5–26 in M.A. Rankin (ed.), *Migrations: Mechanisms and adaptive significance*. Institute of Marine Science, University of Texas, Austin.

Kingsolver, J.G., D.W. Pfennig, and M.R. Servedio. 2002. Migration, local adaptation, and the evolution of plasticity. *TREE* 17(12): 540–41.

Lamborn, R.H. (ed). 1890. *Dragonflies vs. mosquitoes*. New York: D. Appleton & Co.

Lank, D.B., R.W. Butler, J. Ireland, and R.C. Ydenburg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103(2): 303-319.

Latch, E.K., G. Dharmarajan, J.C. Glaubitz, O.E. Rhodes. 2006. Relative performance of Bayesian clustering software for inferring substructure and individual assignment at low levels of population differentiation. *Conservation Genetics* 7, 295–302.

Lockwood, M.W. 2001. *Birds of the Texas Hill Country*. Austin, Texas: University of Texas Press.

Lockwood, M.W., and B. Freeman. *The TOS handbook of Texas birds*. College Station, TX: Texas A&M Press.

Lott, C.A., T.D. Meehan, and J.A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. *Oecologia* 134(4), 505–510.

Lutz, P.E. 1974. Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura* (Odonata: Libellulidae). *Ecology* 55, 370–377.

Magurran, A. 2003. *Measuring biological diversity*. Boston, MA: Blackwell Publishers.

Matthews, J.H. 2004. Report on *Anax junius* emergence in Caledon, Ontario, in 2003. *Ontario Odonata,* vol. 5.

Matthews, J.H. 2005. Long-distance migration and emergence patterns in *Anax junius*: review of work to date. *Argia* 17(3), 29–30.

Matthews, J.H. In press. "Anthropogenic climate change impacts on aquatic macroinvertebrates: a thermal mass perspective." In *Odonate conservation: climate change impacts and monitoring strategies,* Jürgen Ott, ed. Sofia, Bulgaria: Pensoft Publishers.

Matthews, J.H., S. Boles, C. Parmesan, and T. Juenger. In press. Isolation and characterization of nuclear microsatellite loci for the common green darner dragonfly *Anax junius* (Odonata: Aeshnidae) to constrain patterns of phenotypic and spatial diversity. *Molecular Ecology Notes*

Meehan, T.D., J.T. Giermakowski, and P.M. Cryan. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental and Health Studies* 40(4), 291–300.

Murren, C.J., R. Julliard, C.D. Schlichting, and J. Clobert. 2001. Dispersal, individual phenotype, and phenotypic plasticity. In *Dispersal*, edited by J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols. New York: Oxford University Press.

Needham, J.G., M. J. Westfall, and M.L. May. 2000. *Dragonflies of North America*. Gainesville, FL: Scientific Publishers.

Nicholson, J.R.P., M.G. Savory, J. Savory, M.R. Willis. 1989. Micro-quantity tissue digestion for metal measurements by use of a microwave for an acid-digestion bomb. *Clinical Chemistry* 35(3), 488–490.

Norling, U. 1984a. Life history patterns in the northern expansion of dragonflies. *Advances in Odonatology* 2, 127–156.

Norling, U. 1984b. Photoperiodic control of larval development in *Leucorrhinia dubia* (Vander Linden): a comparison between populations from northern and southern Sweden (Anisoptera: Libellulidae). *Odonatologica* 13, 529–550.

Norvell, R.E., F.P. Howe, and J.R. Parrish. 2003. A seven-year comparison of relative-abundance and distance-sampling methods. *The Auk* (120(4): 1013–28.

Odling-Smee, F.J., K.N. Laland, M.W. Feldman, and L.J. Schaaf. 2003. *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.

Palka, D.L. 1996. Effects of Beaufort sea state on the sightability of harbor porpoises in the Gulf of Maine. *Reports of the International Whaling Commission* 46:575-582.

Paulson, D.R. 1966. Dragonflies (Odonata: Anisoptera) of South Florida. Ph.D. Dissertation, University of Miami, 603 pp.

Paulson, D.R., and C.E. Jenner. 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 52: 96-107.

Peakall, R., and P.E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Popuation genetic software for teaching and research. *Molecular Ecology Notes* (6(1), 288–295.

Pfenning, B., and H.J. Poethke. 2006. Variability in the life history of the water strider *Gerris lacustris* (Heteroptera: Gerridae) across small spatial scales. *Ecological Entomology* 31(2), 123–130.

Pritchard, J.K., M. Stephens and P. J. Donnelly, 2000. Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959.

Rankin, M. A., McAnelly, M. L., Bodenhamer, J. E. 1986. The oogenesis-flight syndrome revisted. In Insect flight: Dispersal and migration , ed. W. Danthanarrayana. pp. 27-48. Heidelberg and Berlin: Springer-Verlag.

Rappole, J.H. 1995. *The ecology of migrant birds: a Neotropical perspective*. Washington, DC: Smithsonian Institution Press.

Raymond, M., and F. Rousset. 1995. GENEPOP: population genetics software for exact tests and ecumenism. *Journal of Heredity* 86(3): 248–49.

Ricklefs, R.E. 2000. *The economy of nature*. Fifth edition. New York: W.H. Freeman.

Roff, D.A. 1984. The cost of being able to fly: a study of wing polymorphism in two species of crickets. *Oecologia* 63(1), 30–37.

Roff, D.A. 1994. Habitat persistence the evolution of wing dimorphism in insects. *American Naturalist* 144(5), 772–798.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145:1219-1228.

Russell, R.W. 2005. *Interactions between migrating birds and offshore oil and gas platforms in the northern Gulf of Mexico: Final Report*. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2005-009.

Russell, R.W., M.L. May, K.L. Soltesz, and J.W. Fitzpatrick. 1998. Massive swarm migrations of dragonflies (Odonata) in Eastern North America. *American Midland Naturalist* 140:325-342.

Sagarin, R., and F. Michelli. 2001. Climate change in nontraditional data sets. *Science* 294, 811.

Soltesz, K., B. Barber, and G. Carpenter. 1995. A spring dragonfly migration in the Northeast. *Argia* 7(3):10-14.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 37, 171–214.

Stake, M.M., J. Faaborg, and F.R. Thompson. 2004. The video identification of predators at golden-cheeked warbler nests. *Journal of Field Ornithology* 75(4): 337–344.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/

Trottier, R. 1966. The emergence and sex ratio of *Anax junius* Drury (Odonata: Aeshnidae) in Canada. *Canadian Entomologist* 98, 794–798.

Trottier, R. 1970. Effect of temperature and humidity on the emergence and ecdysis of *Anax junius* (Odonata: Aeshnidae). Doctoral dissertation, University of Toronto, Toronto, Ontario, Canada.

Trottier, R. 1971. Effect of temperature on the life-cycle of *Anax junius* (Odonata: Aeshnidae) in Canada. *Canadian Entomologist* 103: 1671-1683.

Vepsäläinen, K. 1974. The Life Cycles and Wing Lengths of Finnish Gerris Fabr. Species (Heteroptera, Gerridae). Helsinki, Finland: Societas pro Fauna et Flora Fennica.

Waage, J.K. 1979. Dual function of the damselfly penis: sperm removal and transfer. *Science* 203:916-918.

Wadleigh, M.A., J. Veizer, and C. Brooks. 1985. Strontium and its isotopes in Canadian rivers: fluxes and global implications. *Geochimica et Cosmochimica Act* 49, 1727–36.Weir, B.S. 1996. *Genetic data analysis II*. Sunderland, MA: Sinauer Associates.

Walker, E.M. 1958. *The Odonata of Canada and Alaska*. Vol. 2. Toronto: University of Toronto Press.

Waples, R.S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for evaluating the number of gene pools and their degree of connectivity. *Molecular Ecology* 15(6), 1419–1439.

Wassenaar, L.I., and K.A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *NAS Proc* 95(26): 15436-39.

Wassenaar, L.I., and K.A. Hobson. 2000. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39(3), 211–217.

Wassenaar, L.I., and K.A. Hobson. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology* 35(9), 1845–1850.

Webster, M.S., P.P. Marra, S.M. Haig, S. Bensch, and R.T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17(2): 76–83

Weir, B.S. 1996. *Genetic data analysis II*. Sunderland, MA: Sinauer Associates.

Wikelski, M., D. Moskowitz, J.S. Adelman, J. Cochrain, D.S. Wilcove, and M.L. May. 2006. Simple rules guide dragonfly migration. *Biology Letters* 2(3), 325–329.

Williams, C.B. 1957. Insect migration. *Annual Review of Entomology* 2, 163–180.

Williams, D.D. 1997. Temporary ponds and their invertebrate communities. *Aquatic Conservation* 7, 105–117.

Windig, J.J., C.G.F. de Kovel, D. de Jong. 2004. Genetics and mechanics of plasticity. Pp. 31–49, in T.J. DeWitt and S.M. Scheiner (eds), *Phenotypic Plasticity: Functional and Conceptual Approaches*. New York: Oxford University Press.

Wirth, T., and L. Bernatchez. 2001. Genetic evidence against panmixia in the European eel. *Nature* 409(6823), 1037–1040.

Wissinger, S.A. 1988. Life history and size structure of larval dragonfly populations. *Journal of the North American Benthic Society* 7, 13-28.

Wright, S. The genetical structure of populations. *Annals of Eugenics* 15, 323–354.

Zera, A. J., and G. L. Cisper. 2001. Genetic and diurnal variation in the juvenile hormone titer in a wing-polymorphic cricket: Implications for the evolution of life histories and dispersal. *Physiol. Biochem. Zool.* 74:293-306.

Zera, A.J., and L.G. Harshman. 2001. The physiology of life-history trade-offs in animals. *Annu. Rev. Ecol. Syst.* 32:95–126.

Zera, A.J., and R.F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* 42, 207–230.

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